

Craniofacial Morphology of the First Americans: Pattern and Process in the Peopling of the New World

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KEY WORDS Paleoindians; craniometrics; peopling of the Americas; ancient population structure; multivariate analysis

ABSTRACT The peopling of the New World has been the focus of anthropological attention since the last century. Proponents of multiple migration models have claimed that patterns of variation among extant New World populations reflect ancient, discrete migrations to the Americas during the terminal Pleistocene. Although multiple migration models appear to explain patterns of both past and present craniometric variation, this interpretation rests on a number of key assumptions that require further investigation. We examined a series of Paleoindian ($n = 11$) and Archaic ($n = 384$) crania from North and South America, and compare these early samples to a large world-wide sample of late Holocene ($n = 6,742$) remains to assess within- and among-group variability in early samples, and to determine how patterns of variation could be viewed as a reflection of both population history and population structure. Analyses included univariate and multivariate analysis of variance, principal component analysis, calculation of biological distances, and multivariate allocation methods. We also performed model-bound analyses of these data, including Relethford-Blangero analysis and calculation of F_{ST} . Our results indicate that under the assumptions of migration/founder models, the data are consistent with Paleoindians having derived from an undifferentiated Asian population that was not ancestral to modern American Indians. This view can be accommodated into existing models of multiple founders (migrations) in the New World. However, the assumptions required for such an interpretation are not realistic, and the diversity of early populations could as easily reflect population structuring processes such as genetic drift, demographic growth, and other phenomena. When the data were analyzed controlling for the effects of genetic drift (i.e., with smaller long-term effective population sizes for Paleoindians), the Paleoindian samples were no longer distinct from modern Native American populations. Other factors that need to be considered include processes involved in craniofacial change and adaptation during the past 10,000 years. Finally, patterns of variation in the North and South American Paleoindian samples are different, suggesting that the process of New World colonization is more complex than previously assumed. *Yrbk Phys Anthropol* 42:153–188, 1999. © 1999 Wiley-Liss, Inc.

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The origin of Native Americans has been a topic of discussion among Americanist scholars since the sixteenth century, where proponents of the Garcian and Acostan traditions argued whether American Indians arrived in the New World from Phoenicia, Spain, or even Atlantis, or came to the New World using a yet to be discovered overland connection between Asia and America (Huddleston, 1967). Although a trans-Atlantic migration model has seen a resurgence in the popular press (Begley and Murr, 1999), most researchers working on the origin of American Indians continue to hold the view first presented by Acosta: that living and past peoples of the New World are derived from late Pleistocene populations of east Asia.

While the timing of colonization now appears to be closer to resolution (Dillehay, 1999; Meltzer et al., 1997), questions regarding the number of founding migrations to the Americas are far from resolved (Dillehay, 1999; Steele and Powell, 1993; Szathmáry, 1993a,b). Anthropologists have examined genotypic and phenotypic variation among past and present Native Americans, in hopes that these data might provide more informative evidence of prehistoric popula-

tion dispersal and evolution than is possible using the archaeological record alone. Accordingly, biological anthropologists have employed a wide range of phylogenetically informative data to provide support for various models of peopling of the new world. These data include dental morphology (Greenberg et al., 1986; Hanihara, 1968; Haydenblit, 1996; Powell, 1995, 1997; Powell and Neves, 1998; Sutter, 1997; Turner, 1985, Turner and Bird, 1981), nuclear and mitochondrial genetic markers (Bonatto and Salzano, 1997; Cann, 1994; Fox, 1996; Greenberg et al., 1986; Horai et al., 1993; Kolman et al., 1995, 1996; Merriwether et al., 1995; O'Rourke et al., 1992, 1999; Pena et al., 1995, 1997; Schanfield, 1992; Stone and Stoneking, 1996, 1998; Szathmáry, 1993b, 1994; Szathmáry and Ossenberrg, 1978; Wallace and Torroni, 1992), and skeletal morphology (Birdsell, 1951; Genovés, 1967; Hrdlicka, 1907, 1913, 1920, 1923; Jantz and Owsley, 1997; Jantz et al., 1992; Konigsberg and Ousley, 1993, 1995; Neumann, 1952; Neves and Pucciarelli, 1989, 1991; Ossenberrg, 1994; Steele and Powell, 1992, 1993, 1994; Stewart, 1957, 1981; Szathmáry and Ossenberrg, 1978).

At the heart of the debate is whether Native Americans¹ are biologically, linguistically, and culturally homogeneous, and how any observed variation should be interpreted in an evolutionary context (Genovés, 1967). Initial observations of limited biological variation among Native Americans prompted speculation that such shared characteristics as hair type and skin color reflected common descent from a single founding population, and that New World peoples "constituted a major isolate that was homogeneous, both phenotypically and genotypically" (Stewart, 1960, p. 269). Other researchers observed biological heterogeneity among American aboriginal populations, and attributed the among-group differences to multiple, distinct founding populations (Greenberg et al., 1986; Munford et al., 1995; Rivet, 1943; Turner, 1985). Still others recognized that in addition to migration,² other evolutionary forces such as genetic drift, natural selection, or in situ gene flow helped to explain the observed patterns of variation (Stewart and Newman, 1951; Spuhler, 1979; Szathmáry, 1994) and confounded simple explanations that invoked migration as the sole source for patterns of modern variation in the New World.

While the above-cited studies provide considerable evidence for modern patterns of variation, most do not directly address the biological variation of the founders themselves. However, new discoveries of ancient skeletons in the Americas, redating of existing skeletal series (Dansie, 1997; Kirner et al., 1996), and reanalyses of ancient remains excavated earlier this century (Jantz and Owsley, 1998; Munford et al., 1995; Neves and Pucciarelli, 1989, 1991; Neves et al.,

1996a,b, 1998; Powell and Steele, 1993; Steele and Powell, 1992, 1993, 1994) have resulted in a collection of early skeletons that is growing not only in size, but also in importance for our understanding of past and present phenotypic variation in the New World.

In this paper we examine models of colonization derived from ancient American craniometric variation, and present new analyses of the small but important sample of early Holocene populations in North America as a means of exploring temporal and spatial variation. More importantly, we wish to examine how altering the fundamental assumptions used to interpret these data changes our perspective on the colonization process. Although there is a substantial and ever-growing body of literature on genotypic variation among ancient and modern populations in the New World (Bonatto and Salzano, 1997; Cann, 1994; Fox, 1996; Kolman et al., 1995, 1996; Merriwether et al., 1995; O'Rourke et al., 1999; Pena et al., 1995, 1997; Schanfield, 1992; Stone and Stoneking, 1996, 1998; Szathmáry, 1993b, 1994; Starikovskaya et al. 1998; Wallace and Torroni, 1992), and on interpretations of linguistic and archaeological variation in the Americas (Greenberg and Ruhlen, 1992; Nichols, 1990), we do not address those lines of evidence. Instead, we chose to focus on craniofacial variation among past and present American populations, an important line of evidence that has been at the center of anthropological debate for over a century (Hrdlicka, 1913, 1920, Stewart and Newman, 1951; Genovés, 1967), but recently has been eclipsed by developments in the field of molecular genetics (Hagelberg, 1994; O'Rourke et al. 1999; Stone and Stoneking, 1996, 1998; Szathmáry, 1993b).

One potential drawback to analyses of craniofacial morphology used for the reconstruction of population relationships is that craniofacial form is partly affected by environmental constraints. Although *direct* evidence for the effects of selection on craniofacial shape have not been well-proven (Relethford, 1994), indirect evidence such as temporal and spatial trends in craniofacial dimensions have been documented (Boyd, 1988; Brown, 1987; Carlson and Van Ger-

¹We use the term "Native American" here to denote all indigenous peoples of the Americas. In order to distinguish arctic (Aleuts and Eskimos) and Na-Dene speaking populations from other native groups in North and South America, the term *Amerindian* will be used to designate the latter. Although this division generally follows that of Greenberg (1987) and Greenberg et al. (1986), it is used here as a matter of convenience rather than as indicative of historical or phylogenetic relationships.

²The term "migration" creates some confusion, since most models of "migration" to the New World actually refer to diffusion events in which different and distinct populations colonize/invoke new territory. We use the term "migration/founder model" as synonymous with a nonrecurrent historical range expansion, and distinguish it from gene flow (also referred to as "migration") in population genetics models. Migration models in population genetics attempt to measure the effects of gene flow and genetic drift on population structure.

ven, 1977; Weidenreich, 1945), and are reviewed by Larsen (1997). Anthropometric assessments of craniofacial form in the Americas have shown a relationship between measures of facial height and climate, at least as reflected in the geographic positions of the populations examined (Jantz et al., 1992). Kean and Houghton (1990) observed that the distinctive facial form of Polynesian populations reflects the development of the cranial base, the short load arm of the mandible, and their subsequent effects on facial prognathism and positioning. Australian populations, which have shorter upper facial heights and larger teeth, also exhibit pronounced midfacial prognathism and average cranial base flexure. Thus facial forwardness is, in part, a reflection of masticatory constraints of the load arm of the mandible and tooth size (Kean and Houghton, 1990). Differences in craniofacial form among temporal samples in a region have been interpreted as the result of changes in functional loading of the teeth and jaws (Boyd, 1988; Carlson and Van Gerven, 1977; Weidenreich, 1945) or even as a physiological response or adaptation to changes in temperature during the Holocene (Brown, 1987). Regardless of the cause of patterns of change, there are clearly functional, developmental (Enlow, 1990), and adaptational factors that affect human craniofacial morphology through gene-environment interactions (Crawford, 1999, p. 237).

Analyses of craniofacial variation among ancient and modern human populations, despite the above limitations, have the potential to provide important information about past population structure,³ demography, and history. Recent advances have improved our understanding of the genetics of complex morphological features (Richman, 1995; Weiss, 1993), and new theoretical approaches allow the application of quantitative genetic methods to traditional skeletal (Konigsberg, 1990; Konigsberg and Blangero, 1993; Lynch, 1989; Relethford, 1994, 1995; Relethford and Harpending, 1994, 1995; Rogers et al.,

this volume) and anthropometric (Konigsberg and Ousley, 1993, 1995; Relethford, 1992; Relethford and Blangero, 1990; Relethford and Lees, 1982; Relethford et al., 1997; Williams-Blangero and Blangero, 1989) data. As the sample size for early American skeletons grows, we are able to ask more complex questions of these data by applying new approaches. More importantly, additional discoveries of ancient skeletons in the New World require that we reexamine our models, assumptions, and methods. Current discussions of Native American origins, centered on issues of data interpretation and opposing theoretical standpoints, have a rich and deep history in American biological anthropology.

HISTORICAL PERSPECTIVES ON NEW WORLD BIOLOGICAL DIVERSITY

Migrationist models

One of the earliest and most influential European assessments of Amerindian biological and cultural variation was that of Christopher Columbus, who wrote in 1492 that "In all these islands, I saw no great diversity in the appearance of the people or in their manners and language. On the contrary they all understood one another" (Colón, 1966, pp., 196–197). Stewart and Newman (1951), in their important historical overview of the concept, traced the European view of Native American biological homogeneity not to Columbus, but to the writings of the eighteenth-century Spanish traveler Antonio de Ulloa: "Visto un Indio de qualquier región, se puede decir que se han visto todos en quanto al color y contextura" (Ulloa, 1944), which has become the vituperative English adage "If you've seen one Indian, you've seen them all."

By the late nineteenth century this statement had become an unshakable axiom in scientific circles, principally because it was supported by observations of phenotypic traits that exhibited relatively little variation, such as hair form and color, presence of epicanthic folds, and skin color (Stewart and Newman, 1951). Ulloa's comments on within-group biological homogeneity were further supported in Samuel Morton's (1839) *Crania Americana*, in which he reiterated Ulloa's statement and made an attempt to

³Population structure refers the apportionment of genetic variation among interbreeding demes due to *processes* such as gene flow and genetic drift. Population history refers to genetic changes attributable to nonrecurrent historic *events* such as range expansion, range contraction, and population replacement (Templeton et al., 1995).

justify this view using craniometric data of dubious quality (Gould, 1993). Several researchers following Morton observed that American Indian crania could be subdivided into distinct "types" that exhibited relative within-group homogeneity but considerable between-group variation (Neumann, 1952).

The observed phenotypic uniformity within subdivisions of living Native Americans was interpreted as the result of discrete migrations from the Old World. Similarities in speech, behavior, or biology could not have arisen through in situ processes because, according to the accepted view as late as the 1920s, American Indians had been in the New World only a few thousand years, and therefore constituted one distinct "race" unified by descent from an ancestral migrant population. Many anthropologists and biologists not only tended to lump various Native American populations together, but assumed that natural selection and other evolutionary processes, while playing a role in shaping other species, minimally affected anatomically modern humans (Stewart and Newman, 1951). Thus, any differences between populations were felt to reflect *independent* migrations of people from the Old World. Most anthropologists "disavowed the possibility that physical changes could have occurred among New World peoples" (Stewart and Newman, 1951, p. 21). Such views were well-suited to classification schemes and typologies, which tended to view populations as internally static (Schindler, 1985), changing primarily as a result of admixture of various "types" or races (Neumann, 1952). Polyracial migrationist models in the extreme appear in Harold Gladwin's (1947) *Men Out of Asia*, which suggested that the New World was populated by as many as six waves of migration: two "Australoid" groups (representing Clovis and Folsom cultures), Algonquian, Eskimo, Mongoloid, and finally a trans-Pacific Polynesian/Arawak migration.

Microevolutionary models

The concept of Amerindian biological unity gained widespread popularity in the 1800s and early 1900s due, in part, to the influence of Morton and Hrdlicka. However, this view did not go unchallenged. Several early writers and naturalists such as d'Orbigny (1839)

and von Humboldt (1811) felt that there was tremendous biological diversity among living Native Americans, despite the obvious but superficial phenotypic similarities of skin color or hair type (Hooton, 1946). Scholars examining the biology of Native Americans also observed extensive inter-tribal biological diversity and generally dismissed the idea of Native Americans as a unified population (Boas, 1912a,b; Dixon, 1923; Hooton, 1930; Virchow, 1888; Wilson, 1857).

Underpinning these alternative conclusions was the recognition that biological variation appeared to be correlated with cultural or environmental conditions, suggesting that biological differences among Native Americans might be due to normal developmental and evolutionary processes rather than solely the result of past migrations (Stewart and Newman, 1951). Some researchers, including Boas (1912a,b), attempted to reconcile the migrationist approach of the classifiers with models of in situ biological change resulting from natural selection and "local differentiation" (the latter term was similar in usage to the modern concept of genetic drift, although this concept had yet to be formally defined by Sewall Wright). Though Boas thought that Native Americans originated through one or more migrations that introduced some variation to the New World (Boas, 1912a), he also felt that once a founder group or groups settled in the Americas, "the isolation and small number of individuals in each community gave rise to long-continued inbreeding and with it to a sharp individualization of local types. This was emphasized by subtle influences of natural and social environment. With the slow increase in numbers, these types came into contact; and through mixture and migration a new distribution of typical forms developed" (Boas, 1912b).

Although Boas recognized that migration and founder effect played a role in shaping the appearance of native populations, he allowed that other evolutionary forces and environmental differences could also bring about divergence. Most importantly, Boas (1912b) recognized that population growth and gene flow could also lead to temporal changes in phenotypic variation among members of a biological lineage. In later

research, Hrdlicka (1935) addressed the question of multiple migrations to the New World, and criticized those claiming that differences observed in some early South American crania represented the presence of pre-Columbian African "types" in the New World:

"One of the greatest faults and impediments of anthropology has always been and is largely to this day, in spite of ever-growing evidence to the contrary, the notion of the permanence of skull types, and of their changeability only through racial mixtures or replacements. It is time that this attitude be replaced by more modern and rational views on the subject, based on the steadily increasing knowledge of biological laws and processes, together with such powerful factors as segregation and isolation" (Hrdlicka, 1935).

MODERN VIEWS OF THE PEOPLING OF THE NEW WORLD

The debate over Native American phenotypic variation and its interpretation continues today, and has been reviewed by several authors (Genovés, 1967; Meltzer, 1993a,b; Schindler, 1985; Stewart and Newman, 1951; Szathmáry, 1993a). A number of biological anthropologists, geneticists, and linguists maintain the view that Amerindians, Aleuts, Eskimos, and Athabaskan (Na-Dene) populations in the Americas each form a homogeneous population [see, for example, references in Genovés (1967), Greenberg et al. (1986), and Stewart (1960)] distinct from the other lineages, although there is disagreement over how these groups may be interrelated (Greenberg et al. 1986; Szathmáry and Ossenberg 1978). The biological homogeneity of Amerindians (excluding Na-Dene and Arctic peoples) has been interpreted as a direct reflection of a late Pleistocene migration from Asia, so that all living Amerindians are descendants of a small founding population and thus share certain phenotypic and genotypic traits (Hrdlicka, 1920; Turner, 1985, 1992) as well as linguistic features (Greenberg, 1987; Greenberg and Ruhlen, 1992; Greenberg et al., 1986). On the other hand, many linguistic, genetic, skeletal, and dental studies indicate that the Amerindian "group" is more variable and diverse than would be expected from a single, recent migration (Haydenblit, 1996; Horai et al., 1993; Lahr, 1995; Neves and Pucciarelli, 1991; Nichols, 1990; Schanfield, 1992;

Steele and Powell, 1993, 1994). Most scholars agree that humans in the New World did not develop in this region from earlier forms of *Homo* or other extinct hominid taxa, but instead arrived via migration from east Asia (Lahr, 1996), a view presciently espoused by Fray Jose de Acosta nearly 500 years ago. The real question is how to interpret patterns of past and present genotypic and phenotypic diversity within the context of one or more Old World founding events (migrations), and the extent to which other evolutionary forces contributed to the variation we do see.

Multiple migration/founder models

Perhaps no other recent model of the peopling of the New World has generated more discussion than the tripartite model presented by Greenberg, Turner, and Zegura (1986). The tripartite model employed independent lines of linguistic, genetic, and dental variation to propose that all Native American populations derived from one of three migratory movements (i.e., range expansions) between northeast Asia and the Americas during the late Pleistocene. In their findings, the authors noted that Aleut and Eskimo populations form a distinct group, as did Na-Dene speaking populations (Haida, Tlinkit, Athabaskan). Turner (1985, 1989, 1990, 1992) observed that two major dental patterns were present in Asia during the terminal Pleistocene, which could be used to trace evolutionary histories of Asian and Asian-derived populations under the assumption of a slow rate of dental evolution (Powell, 1993; Turner, 1986). Sinodonts, characterized by "intensified" dental features such as incisor shoveling, first occupied northern Asia during the late Pleistocene, having derived from an earlier Sundadont population in southeast Asia. Sundadont teeth exhibited fewer of these "intensified" features. Early Holocene Paleoindians⁴ in

⁴The term "Paleoindian" is used by most authors to refer to populations of the late Pleistocene and early Holocene (12,000–8,500 years B.P.) in the Americas thought to be associated with the Clovis, Folsom, and Cody archaeological complexes (Meltzer, 1993a), although this time span also includes archaeological horizons referred to as early Archaic (Steele and Powell, 1992). Other researchers, referring to late Pleistocene and early Holocene populations in the New World use terms such as "First Americans" or "Paleoamericans" (Jantz and Owsley, 1997; Steele and Powell, 1999) to avoid implying that these early populations

the Americas were thought to have been derived from a wave of Sinodont migrants, since in Turner's view, the Upper Cave 101 skeleton from Zhoukoudian, China exhibited Sinodont features at a presumed date of 20,000 years B.P. (although this date has now been questioned; see Kamminga, 1992; Kamminga and Wright, 1988; and Lahr, 1996). Thus the descendants of Paleoindians all shared the Sinodont pattern due to recent common ancestry, and spoke languages classified by Greenberg as part of the "Amerind" family. Turner also noted that Na-Dene speakers had common dental features separating them from Amerindians and from later and more dentally and linguistically distinct Aleut-Eskimo populations. The dental, linguistic, and to a lesser extent, genetic data supported the separate Amerind, Na-Dene, and Aleut-Eskimo linguistic groupings; the authors viewed this as evidence for three separate waves of migration (Greenberg et al., 1986).

Although there was some limited ancillary support for this view (Cavalli-Sforza et al., 1994; Williams et al., 1985), the weight of opinion at the time and subsequently has not supported the tripartite model (Crawford, 1998; Merriwether et al., 1985; Powell, 1995; Stone and Stoneking, 1998; Szathmáry, 1986, 1993, 1994; Szathmáry and Ossenberg, 1978; Weiss 1994; Weiss and Wolford, 1986). Critics have pointed out that there is no direct correspondence between language and biology (Goddard and Campbell 1994; Weiss and Wolford, 1986). In addition, mtDNA and immunoglobulin analyses showing the uniformity of the Amerind group were based on the assumption that the founding population was not polymorphic, so that the constructed phylogenetic history of a population corresponds to the initial diversity at a single locus (Szathmáry, 1993a,b, 1994).

Multiple migration/founder alternatives to the tripartite model have been presented by Horai et al. (1993), Karafet et al. (1999), Neves and Pucciarelli (1991), Schanfield (1992), Schurr et al. (1999), Starikovskaya et al. (1998), Wallace and Torroni (1992),

and others. These alternatives propose two or more waves of Asian migration, with many focusing on at least four New World founding events (Horai et al., 1993; Neves and Pucciarelli, 1991; Schanfield, 1992; Schurr et al., 1999, Starikovskaya et al., 1998; Wallace and Torroni, 1992). Horai and co-workers (1993) noted that mtDNA variation within the tripartite model's "Amerind" group represents at least four separate founding lineages. Likewise, other researchers dealing with mtDNA have noted multiple founding lineages in the Americas (Schurr et al., 1999; Starikovskaya et al., 1998; Wallace and Torroni, 1992). Researchers dealing with geographic patterning in Y chromosome (Karafet et al., 1999) and mtDNA (Templeton, 1998a,b) variation have employed a novel phylogenetic method (Templeton et al., 1995) for detecting range expansions and restricted gene flow among Native American populations. The mtDNA data (Templeton, 1998a) indicate either more than one colonization event, a large colonizing population, or an extended colonization process that resulted in significant haplotype diversity in the Americas. The Y chromosome data suggest a colonization/range expansion out of Asia that brought haplotype 1F to both Australasia and the New World, followed by a range expansion in Siberia that brought haplotype 1C to the New World (Karafet et al., 1999). However, these authors note that extensive gene flow within Asia, on Beringia, and subsequently in the New World may have significantly complicated the interpretation of phylogenetic patterns in these data.

Neves and Pucciarelli (1991) presented a "four-wave" model of colonization that simply added an additional migration event to the three proposed in the tripartite model. The four-wave model was based on the distinctive "non-Mongoloid" morphology of the earliest crania in South America that, according to these authors, differ too greatly from late Holocene "Mongoloid" populations in the New World (represented by Amerind, Na-Dene, and Aleut-Eskimo groups) to be explained by an ancestral-descendant relationship between them (Neves et al., 1996a,b). Here the term "Mongoloid" was used to denote late Holocene populations of

were ancestral to modern Native American populations. The term "Archaic" is used here to refer to populations of the middle and late Holocene (8,500–3,000 years B.P.).

northeast Asia and the Americas, who share certain phenotypic features such as facial flatness, epicanthic folds, and shovel-shaped incisors (Hanihara, 1968; Hrdlicka, 1920; Lahr, 1996; Turner, 1989, 1990) that distinguish them from southeast and southwest Asians. Neves and Pucciarelli (1991) and Munford et al. (1995) postulated that the earliest colonists of the New World were derived from a population of anatomically modern *Homo sapiens* in East Asia that eventually migrated north and south, leaving descendants in Australia and the Americas (as Paleoindians). Sutter (1997) and Haydenblit (1996) have presented dental data to support this view, while Powell's (1995) analysis of North America dental data has been interpreted as supporting a non-Mongoloid presence in the Americas (Lahr, 1997). Schanfield (1992) examined immunoglobulin allotypes for North and South American populations and felt the observed patterns of variation were the result of four major migrations to the New World. Wallace and Torroni (1992) viewed patterns of mtDNA variation as reflecting four founding lineages in the Americas, while Ballinger et al. (1992) observed that the 9 bp deletion present in the Americas also occurs in Australasian groups, suggesting some support for the Neves et al. (1996a,b) version of the four-wave model. Again, critics have pointed out that the problems noted for the tripartite model apply to migrations of four or more groups (Weiss, 1994).

Problems and assumptions of migration

Migration/founder models ultimately have their roots in diffusionism, which is at odds with neo-Darwinian concepts of population variation and adaptation (Lahr and Foley, 1998). Models of colonization and replacement based on skeletal morphology tend to demarcate populations geographically, and give little attention to microevolutionary processes such as gene flow or natural selection, making it seem that such views "have more in common with Elliot Smith's hyper-diffusionism than with modern evolutionary biology" (Lahr and Foley, 1998, p. 143). These models also assume that craniofacial change is not influenced by masticatory change and other epigenetic processes, despite

evidence for such change in other skeletal time series (Boyd, 1988; Brown, 1987; Carlson and Van Gerven, 1977; Weidenreich, 1945). Colonization models used in conceptualizing the peopling of the Americas suffer from these problems of diffusionism and a lack of appreciation for evolutionary change. In particular, they assume that founding populations contained limited internal morphological variation and were therefore phenotypically distinguishable from other such colonizing groups due to the slow rate of evolutionary change for the characters involved (Lahr, 1995, 1997; Neves and Pucciarelli, 1991; Turner, 1989). Migration/founder models also tend to ignore or downplay the role of gene flow and genetic drift in altering or obscuring patterns of population history (Felsenstein, 1982; Relethford, 1995; Wood, 1986).

Several assumptions are required to interpret phenotypic distances as distinct waves of migration. First, the modern population variation must reflect, in some way, ancient founder events, perhaps by freezing ancient population structure with rapid demographic growth. Another assumption is that the ancestral populations were not highly polymorphic or multilingual, so that shared genes or language elements among their descendants reflect common origin rather than convergence due to contact and interaction (Szathmáry, 1994). Furthermore, diachronic changes in language or biology are assumed to be negligible, so that similarities between groups can be interpreted as the product of past historical *events* such as a range expansion or colonization, rather than ongoing evolutionary *processes* such as gene flow, natural selection, language borrowing, or language loss. As Templeton (1998b) and Karafet et al. (1999) note, population history and population structuring processes are non-mutually exclusive, and both may have had a significant impact on the genetic structure of human populations. However, most anthropologists dealing phenotypic data of living peoples in the Americas have tended to focus on the historical aspects, so that differences among modern groups can be interpreted as a result of different "waves of migration" from Asia (Greenberg et al., 1986; Neves et al., 1996; Turner, 1985).

Biological variation in recent (i.e., late Holocene) Native American populations is, however, a product of *all* evolutionary processes that have acted on them up to that point (Schindler, 1985; Spuhler, 1979), and not just historical range expansions (Templeton, 1998b; Templeton et al., 1995). Native American populations experienced dramatic changes in population size after European contact (Ubelaker, 1992), as well as gene flow with other native and non-native groups (Salzano and Callegari-Jacques, 1988) and demic extinctions. All of these factors may have had a significant impact on the genetic structure of modern Native American populations (Crawford, 1998). Furthermore, changes in mastication, diet, and other cultural factors may have had an impact on craniofacial morphology in Native American populations (Boyd, 1988). Several authors working on early to late Holocene variation have observed significant changes in the neurocranium and splanchnocranium that may be the result of changes in patterns of growth (Enlow, 1990), mastication and diet (Boyd, 1988; Carlson and Van Gerven, 1977; Weidenreich, 1945), and climatic adaptation (Brown, 1987; Jantz et al., 1992).

Another problem is that in order to interpret phenotypic distances as a reflection of population history, we must assume that the characters under consideration are evolving at an equal rate across all groups. Most studies (Lynch, 1989; Relethford, 1994, 1995; Relethford and Harpending, 1994, 1995) have made this assumption, and in order to simplify our analyses, we follow this approach. We must further presume that there is some discernible genetic signal underlying the phenotype in question. Devor (1987) provided estimates of heritability for anthropometric dimensions of the face and head, which Relethford (1995) averaged to $h^2 = 0.55$. In a study of craniofacial variation derived from lateral cephalograms of siblings pairs, Najem (1997) produced h^2 estimates ranging from as low as 0.03 to as high as 1.0, with an average for cranial dimensions of $h^2 = 0.69$. Thus the proportionality of genotypic and phenotypic variance seems to be a reasonable assumption, as noted by Konigsberg and Ousley (1993, 1995). Finally, the traits under consideration also

must not reflect natural selection (Relethford and Harpending, 1995). Despite some difficulties, the interpretation of past and present human craniometric variation does have the potential to reveal information about population history and structure. The difficulty lies in determining which of these — history, structure, or both — we are actually observing in our data.

EARLY HOLOCENE PHENOTYPIC VARIATION

Since the late nineteenth century, biological anthropologists have been concerned with the variation presented by ancient American skeletal remains. Several skeletons, including the Calaveras, California skull, and the pelvis from Natchez, Mississippi, were thought to provide evidence of an “archaic” population in the Americas prior to the last glaciation (Steele and Powell, 1999), although they were dismissed by Hrdlicka as morphologically modern (Hrdlicka, 1907, 1923, 1937). Jenks’ (1937) analysis of the “Minnesota Man” skull, now known as the Pelican Rapids female (Steele and Powell, 1992), suggested an unusual, differentiated, and possibly non-Asian origin for this early skeleton. Researchers examining what are now considered to be early and middle Holocene crania from central Brazil, the Texas coast, and lower California, noted resemblances between these crania and those from late Holocene populations in Melanesia (Dixon, 1923) and Easter Island (Oettinger, 1934, cited in Hrdlicka 1935). Rivet (1943) proposed that this similarity must be the result of direct migration of Australian populations to the Americas, a finding reiterated by Gladwin (1947). However, most researchers dismissed direct contact between Melanesia and the Americas (Dixon, 1923; Hrdlicka, 1935). Hooton (1930) and Neumann (1952), in observing variation in New World crania, suggested that the observation of different “types” among New World populations was the product of multiple Old World migrations to the Americas. Neumann (1952) identified ten varieties, or “local races” among North American crania that could be joined into one of two groups — the Paleoamerinds, who were dolichocephalic with delicate facial features, and the Cenoamerinds, who

were brachycephalic with more robust facial features. These two major types were thought to reflect two separate migrations from east Asia (Neumann, 1952).

Most recently, attention has focused on dating existing collections (Dansie, 1997; Kirner et al., 1996) and on re-examining the existing well-provenienced late Pleistocene and early Holocene skeletons in the Americas (Neves and Pucciarelli, 1989; Steele and Powell, 1992, 1994; Turner, 1985, 1992; Turner and Bird, 1981). The interpretation of these remains differs considerably across studies. Turner (1985, 1992) and Turner and Bird (1981) noted that Paleoindian dental samples represent a Sinodont pattern reflecting their origin from a northeast Asian source population, although some degree of Sundadonty was observed for some individuals (Turner, 1985, 1992a,b; Turner and Bird, 1981). Likewise, Powell (1993, 1997, in press; Powell and Neves, 1998) observed that Paleoindian teeth exhibit a mix of features found in both northeast Asian (Sinodont) and southeast Asian (Sundadont) populations, while Haydenblit (1996) found that early samples from Mesoamerica tended toward Sundadonty.

Neves and co-workers (Neves and Pucciarelli, 1989, 1991; Neves et al., 1996a,b, 1997, 1998, 1999a,b), along with their students (Munford et al., 1995), began a systematic study of craniometric variation in South America during the late 1980s. In their multivariate analyses, they demonstrated, as previously observed by Dixon (1923) and Hrdlicka (1935), that lowland Paleoindians from Brazil were morphologically distinct from modern American Indians and northeast Asians, and were morphologically similar to populations from Australia and Africa (Neves et al., 1998, 1999a,b). They proposed that this pattern of Paleoindian differentiation represents a wave of non-Mongoloid migrants from east Asia (Neves et al., 1996b), who were derived from a generalized morphology common to east Asia and Australia during the terminal Pleistocene (Kamminga, 1992; Lahr, 1995, 1996; Neves et al., 1999a,b). Based on their analyses, they suggested that only during the middle Holocene did "Mongoloid" populations enter the Americas, followed by Na-Dene and Aleut-Eskimo

groups (Lahr, 1996; Neves et al., 1996, 1998). When compared to later Archaic samples from South America they observed a clear morphological break with no evidence for phenotypic continuity over time between groups. Support for this view comes from the observation of non-Amerindian craniofacial morphology among early skeletons in North America (Jantz and Owsley, 1997; Steele and Powell, 1992, 1993, 1994; Powell and Steele, 1993), as well as from patterns of genetic (Cann, 1994; Fox, 1996; Horai et al., 1993) and dental (Haydenblit, 1996; Sutter, 1997) variation South America.

Steele and Powell (Powell and Steele, 1993; Steele and Powell, 1992, 1993, 1994, 1998) have examined the majority of crania in North America dated to between 8,000 and 10,000 years B.P. Like Neves, they performed a series of multivariate analyses on these data, and observed that the craniofacial variation represented by a small sample and a reduced set of variables suggested that Paleoindian crania were distinct from late Holocene American Indians in their reference sample. Paleoindians displayed longer, lower cranial vaults and taller, more narrow faces than modern populations (Steele and Powell, 1992, 1994). Their results did, however, suggest that some Archaic samples shared these same features (Steele and Powell, 1992) suggesting a degree of biological continuity through at least the middle Holocene. When Pleistocene samples from the Old World were incorporated into the analysis, they found that the crania of Paleoindians and Old World late Pleistocene skeletons could not be considered "classically" northeast Asian (Steele and Powell, 1994). Similar results were obtained by Ozolins and co-workers (1997) using a world-wide sample of late Pleistocene and modern crania.

In their analyses of the more complete crania from Spirit Cave and Wizard's Beach sites in Nevada, dated to 9,200 years B.P., Steele and Powell found that these early crania were peripheral to a reference sample of modern American Indians and northeast Asians ($N = 6$ populations), and fell closer to the multivariate space occupied by southern Asian, Pacific, and Australian populations. They also noted that these two Paleoindian

crania are themselves well separated in a principal component analysis, despite their close geographic and temporal proximity to one another (Steele and Powell, 1999).

Jantz and Owsley (1997), in their assessment of the Spirit Cave cranium, obtained similar, but not identical, results to those of Steele and Powell (1999) using a slightly different method of multivariate analysis. They found that the Spirit Cave mummy exhibited a tendency to be grouped with European and Ainu populations in multivariate ordination. They proposed that while modern North American Indians "lack many of the features associated with modern East Asians," they were derived from populations in Asia that exhibited "incipient Mongoloid" features (Lahr, 1995). The Spirit Cave individual, however, did not appear to have been drawn from such an "incipient Mongoloid" group (Jantz and Owsley, 1997). While Jantz and Owsley (1997) were rightfully cautious in interpreting their results and did not make a claim for European affinity of the Spirit Cave individual, other Paleoindian skulls such as the "Kennewick Man" recently have been described as "Caucasoid" in press reports (Begley and Murr, 1999). This has raised questions regarding the possibility of a direct European contribution to the Americas prior to the arrival of the ancestors of the "typical Mongoloid" groups currently occupying the continent.

Although there are no published data that, to our knowledge, support a direct trans-Atlantic migration route to the Americas (other than early historic Norse occupations in northeastern Canada), several studies have investigated the possible contribution of Eurasian Upper Paleolithic populations to the American gene pool. Kozintsev et al. (1999) examined a large sample of crania from the Old and New Worlds, with attention to Neolithic peoples of Siberia. They noted that the Neolithic populations of Okunev and Sopka do exhibit some "Caucasoid" features, but attribute this to admixture with western European populations after the initial colonization of the Americas. Amerindians, however, were found to be less "Mongoloid" than Siberian populations, and Kozintsev and co-workers (1999) observed a diachronic trend in craniofacial size for both

Old and New World populations (attributed to gracilization) that makes some features "irrelevant for tracing genetical affinities."

Statistical analyses of modern genetic data also fail to support a model of pre-Columbian Caucasoid admixture, as recently noted by Long et al. (1999), while data from Y-chromosome haplotypes suggest that similarities of American Indians and Europeans are due to haplotypes moving both east (to America) and west (to Europe) from a northeast Asian source (Karafet et al., 1999). These studies call into question popular press assertions (Begley and Murr, 1999) that the "first Americans" arrived from Europe, making it less likely that the "Caucasoid" appearance of some early American crania reflects a strong genetic contribution from Pleistocene peoples of western Europe. However, the presence of mtDNA lineage X in some genetic studies (Schurr et al., 1999), with its relatively long branch lengths in phylogenetic trees, suggests that there may have been some common ancestry *ancient* eastern Eurasians and the Pleistocene founders of modern Native American populations. However, direct contributions of genes from Europe are, in our opinion, extremely unlikely.

Even the best provenienced and accurately dated sample of ancient remains poses problems for reconstructing population history in the Americas. Researchers working with late Pleistocene crania (Howells, 1989; Lahr, 1995, 1996; Neves et al., 1999a,b; Kamminga, 1992; Kamminga and Wright, 1988) must continually confront questions about the effects of limited variable sets resulting from poor preservation on their results, and about the representativeness of a particular fossil relative to all individuals in the ancient source population. Thus, our reconstruction of the Pleistocene peopling of the Americas must rely heavily on either (a) late Holocene biological samples as descendent "analogues" of the colonization events/processes, or (b) inadequate and fragmentary data from the fossils themselves, with large standard errors of estimates involved.

Our analyses (Neves and Pucciarelli, 1989, 1991, 1998; Neves et al., 1996a,b, 1999a,b; Powell and Steele, 1993; Powell et al., in press; Steele and Powell, 1992, 1994) and those of others (Fenton and Nelson, 1997;

TABLE 1. *New World Paleoindian remains used in this analysis*

Region	Specimen	Location	N	Median ¹⁴ C age (yr B.P.)	References
North America	Warm Mineral Springs	Florida	1	10,260	Clausen et al., 1975
	Spirit Cave	Nevada	1	9,415	Kirner et al., 1996; Tuohy and Dansie, 1997
	Wizard's Beach	Nevada	1	9,225	Dansie, 1997; Tuohy and Dansie, 1996, 1997
	La Brea	California	1	9,000	Stewart, 1967; this study
	Northwest	Washington	1	8,410	This study
Total:			5		
South America	Santana do Riacho I	Brazil	1	11,380	Prous, 1980, 1986, 1991
	Lapa Vermelha IV	Brazil	1	10,505	Laming-Emperaire et al., 1975; 1979; Prous, 1991
	Cerca Grande No. 6	Brazil	2	9,374	Hurt, 1960
	Cerca Grande No. 7	Brazil	2	9,130	Hurt, 1960
Total:			6		

Jantz and Owsley, 1998, in press; Nelson, 1998) have attempted to deal with these difficulties by repeating analyses with different numbers of variables (Neves et al., 1999b), with a combination of different samples (Nelson, 1998), and with different types of multivariate statistical methods (Jantz and Owsley, 1998; Steele and Powell, 1994). While we acknowledge the limitations of early Holocene data, the correspondence of results across studies, samples, and variable sets argues that these approaches are telling us *something* about the past, although at present larger sample sizes may be required to have the statistical power necessary to accurately distinguish between competing models using fossil evidence alone (Rogers, 1995).

Based on the models presented above, we will use the existing well-provenienced sample of early Holocene and late Pleistocene remains to examine the following questions:

- To what degree are North and South American early Holocene populations craniometrically distinct from late Holocene American Indian, east Asian, and European populations?
- How much phenotypic variation is present among early Holocene crania, and what does this say about New World founding populations?
- What assumptions are inherent in various interpretations of patterns of variation among past and present populations of the Americas, and how does altering these assumptions affect our results?



Fig. 1. Distribution of Paleoindian (circles) and Archaic (triangles) samples used in this study.

MATERIALS AND METHODS

Paleoindian and Archaic samples

The oldest human skeletal remains in the New World date to the late Pleistocene and early Holocene (11,350–8,000 years B.P.) (Table 1 and Fig. 1). Following a number of previous researchers (Green et al., 1998; Munford et al., 1995; Nelson, 1998; Neves and Pucciarelli, 1989; Neves et al., 1999a,b,c; Powell, 1993; Steele and Powell, 1992, 1993,

1994; Turner and Bird, 1981; Turner, 1985), we use the term "Paleoindian" to refer to these late Pleistocene and early Holocene remains, since nearly all are contemporary with terminal Paleoindian and early Archaic archaeological assemblages (Myer and O'Connell, 1997; Powell and Steele, 1994; Steele and Powell, 1992; Tuohy and Dansie, 1996, 1997) or early stemmed projectile points in South America (Dillehay, 1999; Laming-Emperaire, 1979; Laming-Emperaire et al., 1975; Prous, 1980, 1986, 1991). We recognize that other authors have adopted the term "Paleoamerican" to describe these remains (Jantz and Owsley, 1997; Steele and Powell, 1999), partly because of problems of assigning all specimens to the "Paleoindian" time period, and partly to avoid implying that these populations were necessarily ancestral to modern American Indians.

Although only 11 Paleoindian individuals are listed in Table 1, we have examined many other skeletal specimens that may date to 8,000 to 11,000 years B.P. as part of other studies (Munford et al., 1995; Neves and Pucciarelli, 1989, 1991; Neves et al., 1996a,b, 1997, 1998, 1999, in press; Powell, 1997, in press; Powell and Steele, 1993, 1994; Powell et al., in press, n.d.; Steele and Powell, 1992, 1993, 1994). Paleoindian individuals such as the Browns Valley skeleton from Minnesota (Jenks, 1937), the "Buhl woman" from Idaho (Fenton and Nelson, 1998; Green et al., 1998), Wet gravel material from Nebraska (Jantz and Owsley, 1998, in press), skeletons from Tequendama, Columbia (Munford et al., 1995; Neves and Pucciarelli, 1989; Neves et al., 1997), and over 50 mineralized skeletons from the Harold Walter collection in Lagoa Santa, Brazil, were not included due to uncertain archaeological provenience, potential interobserver error, and/or limited number of craniometric variables common to all specimens. The latter factor was perhaps the strongest constraint in selecting our Paleoindian sample. The 11 specimens included here provide the fewest missing values in the data matrix.

For some individuals listed in Table 1 we were able to record up to 60 craniometric dimensions. However, differential preserva-

TABLE 2. List of craniometric variables

Glabella-occipital length (GOL) ¹	Biauricular breadth (AUB)
Basion-nasion length (BNL) ^{1,2}	Orbit height, left (OBH)
Maximum cranial breadth (XCB) ¹	Orbit breadth, left (OBB) ¹⁻³
Maximum frontal breadth (XFB)	Interorbital breadth (DKB) ²
Biasterrionic breadth (ASB) ¹	Nasion-bregma chord (FRC) ¹
Nasal height (NLH) ²	Bregma-lambda chord (PAC) ¹
Nasal breadth (NLB) ¹	Lambda-opisthion chord (OCC) ¹
Bizygomatic breadth (ZYB) ¹	

¹ These ten variables were used for comparison of Paleoindians, Howells data, and Archaic samples.

² Measurement definition varies slightly between Howells (1973, 1989) and Hanihara (1993, 1996, 1997), but observer effects were not statistically significant (see Table 5).

³ Orbital breadth (OBB) defined following Howells (1973) and used only for comparison of Howells data, Paleoindian, and Archaic samples.

tion of the remains, constraints of the comparative data, and the lack of univariate normality for some variables limited our analyses to the 14 craniometric dimensions listed in Table 2. This variable set maximized the completeness of the Paleoindian data matrix, but did not eliminate the problem of missing values altogether. For eleven of 154 data points (14 variables \times 11 observations), we estimated missing values using finite mixture analysis (Donnelly and Konigsberg, 1998) of 100 individuals drawn at random from the total W.W. Howells (1973, 1989) data set. Under a two group mixture model, 90.9% of individuals classified as Paleoindians were assigned to one group, and 99% of late Holocene humans were assigned to the other.

The work of most researchers who deal with late Pleistocene human remains focuses on the relationship between early skeletons and modern human populations (Kamminga and Wright, 1988; Steele and Powell, 1994), with little discussion of how late Pleistocene and early Holocene samples are related to temporally adjacent populations of the middle Holocene (see Brace and Tracer, 1992; Carlson and Van Gerven, 1977; Frayer, 1984; Neves et al., 1997, and the review in Larsen, 1997 for exceptions). Because relatively few analyses of Paleoindian samples have examined their relationship to Archaic period (8,000–2,000 years B.P.) populations in the Americas, we compiled data for 13

TABLE 3. *New World Archaic remains discussed in the text*

Region	Site	Location	N	Median ¹⁴ C age (yr B.P.)	References
North America	Pelican Rapids	Minnesota	1	7,840	Myster and O'Connell, 1997
	Indian Knoll	Kentucky	278	5,302	Webb, 1946
	Bird Island	Florida	6	5,297	Doran, unpublished; Powell, 1995
	Black Earth	Illinois	8	6,327	Jefferies and Lynch, 1983
	Eva	Tennessee	7	7,976	Lewis and Lewis, 1961
	Great Basin ¹	Nevada	18	1,980	Dansie, 1997
	Plains Archaic ¹	Composite	2	5,110	Key, 1983
	Sauk Valley	Minnesota	1	4,000	Myster and O'Connell, 1997
Total:	Windover	Florida	28	8,095	Doran and Dickel, 1988
			349		
South America	Palli Aike Cave	Chile	1	>7,830	Neves et al., in press
	Lapa do Boquete	Brazil	2	>7,000	Neves, unpublished
	Lagoa Santa ²	Brazil	28	>7,200	Neves, unpublished
	Lapa de Confins	Brazil	4	>6,000	Neves and Pucciarelli, 1989, 1991
Total:			35		

¹ Composite sample from various sites in a region.² Composite includes nonmineralized Harold Walter collection.

Archaic samples ($n = 384$) in North and South America (Table 3 and Fig. 1). Although some of these data were obtained from published sources listed in Table 2, many are derived from our own observations of these skeletal series.

Comparative data

Comparative data for late Holocene and modern populations were obtained from two large world-wide samples of human crania analyzed by W.W. Howells (1973, 1986, 1989) and T. Hanihara (1993, 1996, 1997). The Howells data include 57 standard measurements for 36 skeletal series (1,348 males and 1,156 females). These data represent regional phenotypic variation prior to extensive migration and population growth of the last 500 years, and have been used as a representative modern human comparative sample in numerous studies of Paleoindians (Jantz and Owsley, 1998, in press; Munford et al., 1996; Neves and Pucciarelli, 1989; Neves et al., 1997, 1999a,b,c; Powell et al., in press; Steele and Powell, 1992, 1994), as well as in assessments of human cranial variation (Kamminga and Wright, 1988; Lynch, 1989; Franciscus and Long, 1992; Relethford, 1994, 1995, 1996; Relethford and Harpending, 1994, 1995). The Hanihara (1993, 1996, 1997) data represent an even larger series from 300 prehistoric and modern human populations around the world, including a large number of samples from the

Americas, western Asia, Melanesia, and the Far East. While this comparative sample provides greater representation within particular geographic regions than the Howells (1973) data, it is limited by a smaller number of cranial dimensions, small individual sample sizes, disproportionate numbers of males in many samples, and the use of slightly different craniometric landmarks [relative to Howells (1973)] for some traits. As a precaution, analyses were initially performed separately for each comparative data set.

Given the similarity of analyses using the comparative data separately, we chose to pool the comparative data into a single, coherent data set that best represents world-wide geographic patterning of craniometric variation. Because the Howells (1973, 1989) measurement definitions differed slightly from those used by Hanihara (1997), we first selected 11 variables that were defined by identical craniometric landmarks (Table 2) and that represented the basic dimensions of the face and skull. Three additional dimensions [interorbital breadth (DKB), nasal height (NLH), and basion-nasion length (BNL)] were defined differently by the two researchers, but in such a way that the two measurement systems produce very similar and often identical values for most individuals (see Howells, 1973 Appendix for a comparison of measurement definitions in various studies). One final measurement, orbital breadth (OBB), was defined quite differently

TABLE 4. Modern comparative samples by region and sex¹

Region	Samples	Females	Males	Total
Africa	30	244	656	900
Europe	32	239	943	1182
Western Asia	38	46	886	932
Polynesia/Micronesia	19	200	750	950
Australasia	20	214	423	637
Far East				
NE Asia	18	167	462	629
SE Asia	28	82	560	642
Ainu/Jomon	3	40	89	129
Total	49	289	1111	1400
Americas				
Amerindians	27	128	362	490
Northwest/Na Dene	2	2	36	38
Eskimo	2	82	131	213
Total	31	212	529	741
Total	219	1444	5298	6742

¹ See Hanihara (1993, 1996, 1997) and Howells (1973, 1989) for additional descriptions of samples.

in the Howells and Hanihara data (Table 2). For this reason, it was employed only in the generation of typicality probabilities using Howells and Archaic samples for comparison.

Our unpublished work using a series of historic and modern crania from New Mexico confirms that the two measurement systems produced no significant differences for the 14 variables (GOL, BNL, XCB, XFB, ASB, NLH, NLB, ZYB, AUB, OBH, DKB, FRC, PAC, OCC) listed in Table 2, after adjusting for family-wise error. After pooling, cranial series with fewer than eight observations were deleted from the analysis. The pooled data were tested for univariate and multivariate normality following Mardia (1970), and 26 outliers were trimmed. The final comparative data represent 14 craniofacial dimensions for 219 populations ($n = 6,742$ individuals) from seven world regions: Africa, Europe, western Asia, the Far East, Polynesia/Micronesia, Australasia, and the Americas (Table 4). The pooled data were tested for regional and observer effects using univariate and multivariate analysis of variance (ANOVA and MANOVA) as well as Levine and Van Valen tests for heteroscedasticity (Manly, 1994) (see Table 5 below).

American samples. The pooled Howells-Hanihara data contains 31 samples ($n = 741$) from the Americas, which allows us to compare craniometric variation within and

between regions. The North and South American data were subdivided into three major groups that roughly correspond to Greenberg's (1987) hypothesized linguistic families of Amerind, Na-Dene, and Aleut-Eskimo. The small sample identified as Pacific Northwest ($N = 38$) includes a composite series from coastal British Columbia containing individuals thought to be part of Greenberg's "Na-Dene" language group, as well as individuals from coastal Washington, British Columbia, and Alaska presumed to represent prehistoric Athabaskan populations (Table 4). The Pacific Northwest sample may also include some Amerindian individuals. The Eskimo group ($n = 213$) is larger, but contains only eastern Eskimo samples from Greenland and Hudson Bay and no Aleut crania. Szathmáry (1993a), in summarizing research on these arctic populations, noted that Greenland Eskimo have close ties with Inupik groups in Alaska, reflecting their derivation from Thule peoples of the circumarctic. We recognize that these samples may not be the best representatives of the three linguistic families, but they do allow us to conduct, with some limitations, an initial examination of recent craniometric subdivision within the Americas.

ANALYTICAL METHODS

Prior to analysis, all observations were standardized within each sex as a means of eliminating sex-related size variation (Relethford, 1994; Relethford and Harpending, 1994; Williams-Blangero and Blangero, 1989) while retaining size and shape variation. To eliminate the effects of scaling in our analyses, we converted the sex-standardized data to Q-mode variables following Darroch and Mosimann (1985). The resulting transformed data retain shape differences, but do not reflect the effects of isometric size (Jungers et al., 1995). Analyses were performed using both the untransformed and transformed data, but only the Q-mode results are presented here. All P values were adjusted for family-wise error using Šidák single-step adjustment, $P_{\text{adj}} = 1 - (1 - P)^k$ where P is the observed P value and k is the number of comparisons (Westfall and Young, 1993).

Model-free analyses

Paleoindian, Archaic, and modern craniofacial data were analyzed using a variety of "model free" (Relethford and Lees, 1982) univariate and multivariate techniques. Model-free analyses, such as ordination of phenetic distances, do not attempt to recover underlying population structure present in the data and often rely on post-hoc interpretations of variation patterns to infer evolutionary relationships (Powell, 1993, 1995; Relethford and Lees, 1982). Model-free methods do, however, serve as an initial point of departure for examining questions regarding phenotypic variation within and between Paleoindian and later Holocene groups. Following on our previous work (Neves and Pucciarelli, 1989, 1991; Neves et al., 1997, 1999; Powell and Steele, 1993; Powell et al., in press), we performed a principal components analysis (PCA) on the individual Paleoindian specimens in Table 1, as well as on Archaic and pooled modern samples. PCA is a descriptive measure that employs the pooled variance-covariance structure of the total data set without regard for the geographic origin of the samples. The variance structure of the total sample is then converted to a series of orthogonal vectors (the principal components) that summarize variation in craniofacial shape (Manly, 1994). Individual observations can then be plotted by their resulting principal component scores as a means of describing their multivariate morphological relationship to all other observations. Samples or individuals that occupy similar space in the PCA plots are morphologically similar and are considered to be, to some degree, genetically similar under the assumption that genotypic covariance is related to phenotypic covariance in the relationship $\mathbf{G} = h^2\mathbf{P}$ (Cheverud, 1988; Konigsberg and Ousley, 1993, 1995; Williams-Blangero and Blangero, 1989). We favor using PCA over other multivariate methods such as canonical discriminant analysis because it does not exaggerate between-group variation (Jobson, 1992; Kiefer, 1990).

The PCA scores for modern comparative data were summarized in two ways. First, we computed the mean PCA score of each of

the 266 populations and plotted the sample centroids in three dimensions using ordination. This technique provides a visual assessment of overall morphological relationships within and between groups. We also constructed 90% and 68% confidence limits around these PCA scores in each of the seven world-wide geographic regions using a principal axis method (Sokal and Rohlf, 1995). The individual Paleoindian and selected middle and late Holocene PCA scores were displayed relative to the regional confidence ellipses. This method allowed us to evaluate whether Paleoindians fell outside the range of variation observed in modern geographic regions. It also provided a quantitative assessment of Paleoindian relationships to modern populations not possible in a simple visual examination of the centroids. PCA analyses were repeated for the New World data, with samples designated as Paleoindian, Amerindian, Pacific Northwest, or Eskimo. Tests for differences in means and variances among New World samples, and between Archaic and Paleoindian samples were performed using ANOVA and MANOVA, as well as Levene's test for homogeneity of variances (Manly, 1994).

Mahalanobis' generalized distance, D^2 , was computed between each of the modern comparative samples and Paleoindians. The Mahalanobis' distance takes the form

$$D_{ij}^2 = (\mathbf{x}_i - \mathbf{x}_j)' \mathbf{P}_w^{-1} (\mathbf{x}_i - \mathbf{x}_j) \quad (1)$$

where \mathbf{x}_i is a vector of t trait means for sample i , \mathbf{x}_j is a vector of t trait means for sample j , and \mathbf{P}_w^{-1} is the inverse of the pooled within-groups phenotypic covariance matrix for the t traits (Mahalanobis, 1936). Pooling within-group covariance matrices for the n samples assumes that their covariance structures are approximately equal. The distance between individual Paleoindians and the modern reference samples was computed using a modification of the generalized distance, in which the \mathbf{x}_i was replaced by x , the vector of values of a single Paleoindian specimen. Mahalanobis distances computed in this way were used to produce a typicality probability (Albrecht, 1992) for each Paleoindian. The typicality probability describes how "typical" that individual is compared to the range of variation present

in the reference sample, without assuming that the individual was in fact a member of that group. Typicality probabilities were obtained using a chi-square distribution with t degrees of freedom. Because we were interested in examining the typicality probability for Paleoindians and Archaic samples, we were forced by missing values in the Archaic data to limit our analysis to a subset of ten variables noted in Table 2.

Jantz and Owsley (in press) have been critical of previous analyses that pool Paleoindians into a single temporal sample (Steele and Powell, 1992, 1994). To examine the effects of sample pooling, we computed inter-individual generalized distances for all Paleoindian specimens as a means of assessing variation among individuals (Van Vark and Schaafsma, 1992). The inter-individual distance was computed as

$$D_{1,2}^2 = (x_1 - x_2)'P_w^{-1}(x_1 - x_2) \quad (2)$$

where x_1 and x_2 represent the vector of values for individuals 1 and 2, respectively. In this case, the P_w^{-1} is the inverse of the pooled within-group phenotypic covariance matrix derived from the Howells-Hanihara comparative sample for t traits. Although it would be optimal to have some measure of the covariance structure of populations living during the late Pleistocene and early Holocene, sample sizes are too small for the Archaic and Paleoindian groups to provide a representative covariance structure. Instead, we followed Van Vark and Schaafsma (1992) in using modern reference samples as a conservative estimate of the underlying covariance that may have been present among fossil groups. If the variance between fossil populations was greater than that of the modern reference groups, as would be expected in small, isolated Pleistocene populations, then inter-individual distances presented here should be greater than the values obtained using an actual late Pleistocene variance-covariance structure. The within-group covariance matrix, pooled across the seven major world regions, was used in this procedure.

The significance of the inter-individual D^2 values was obtained following Defrise-Gussenhoven (1967), who demonstrated that the value $\sqrt{D^2}$ obtained for a pair of individu-

TABLE 5. MANOVA results for the pooled Howells-Hanihara data¹

Effect	Wilk's λ	F	d.f.	P-value
Region	0.98376	1.1516	81, 36767.86	0.1659
Observer	0.99956	0.2758	9, 5688	0.9813
Observer* region	0.99208	0.7186	63, 32041.22	0.9551

¹ Global interobserver effect: $F = 0.5502$ at 9, 5568 d.f.; $P = 0.8384$.

als drawn at random from a single population is distributed as $\sqrt{(2t-1)}$ with $s^2 = 1$. For this study, using $t = 14$ variables, the test statistic is $\sqrt{(2t-1)} = 5.19615$. Distances greater than this value are considered to be too great to represent individuals from a single population. Prior to applying this method to Paleoindian inter-individual distances, we tested the approach using the Howells (1973) data for Easter Island. The Easter Island sample is known to represent a relatively isolated modern human population with limited long-range gene flow, but some possibility of internal population structure (Stefan, in press). We generated inter-individual distances for the Easter Island sample and tested these using the Defrise-Gussenhoven (1967) method. A random sample of $n = 10$ individuals was drawn from the Howells Easter Island series. The proportion of significant inter-individuals was recorded, and the procedure repeated 1,000 times to determine what proportion of observations from a known population would exhibit significant distance values.

RESULTS

Comparison with modern world-wide samples

The results of ANOVA and MANOVA tests for region, observer, and interaction effects in the pooled Howells-Hanihara data are presented in Table 5. Given the low level of observed interregional craniometric variation among modern humans (Relethford, 1994, 1995), it is not surprising that interregional differences are significant only at the $p = 0.20$ level (Table 5). As expected, there was no significant observer or interaction term in the model. To ensure that differences between observers could in fact be detected, we repeated our analyses using variables in the pooled modern data that were defined with significantly different

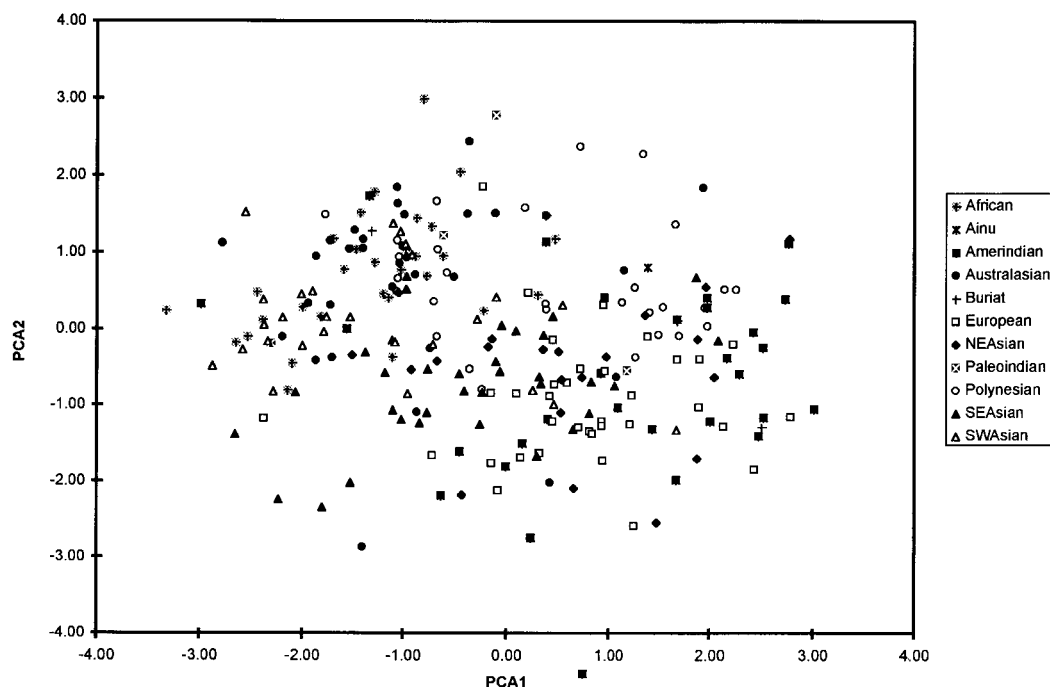
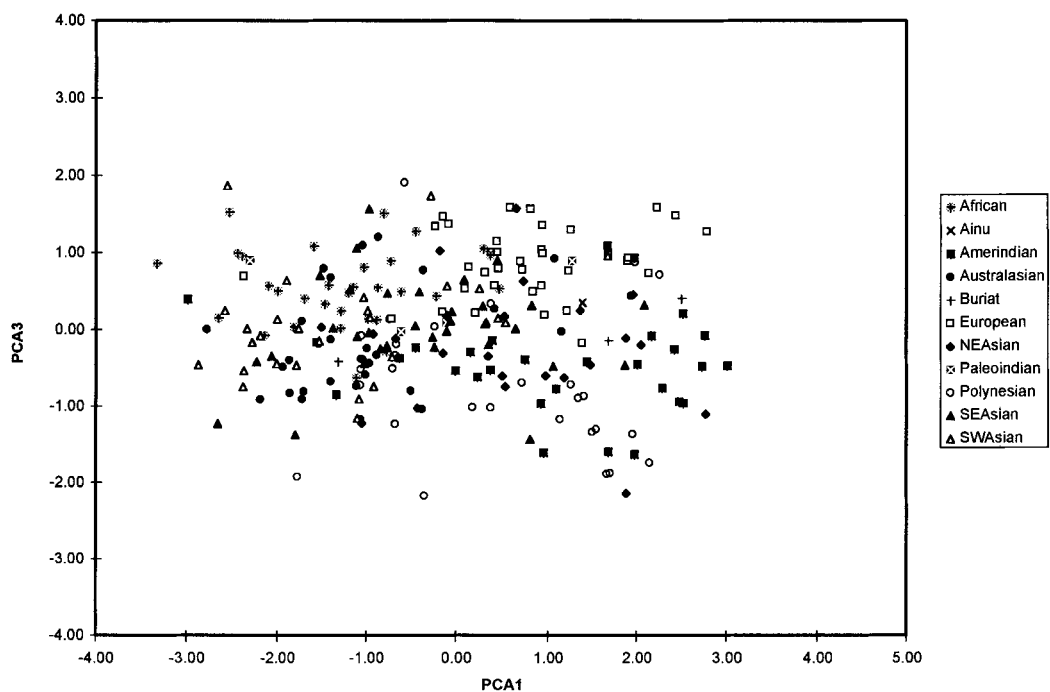
**A****B**

Fig. 2. Principal component plot of early and late Holocene populations using 14 variables. The first three components account for 52% of the variation in the original size-corrected data. Some data points are not shown because they occupy the same portion of the plot. **A:** Plot of the first and second principal components. **B:** Plot of the first and third principal components.

landmarks, such as upper facial height (which uses prosthion or alveolare, depending on the measurement set). As expected, significant interobserver effects were detected for these dimensions but not for the 14 variables in Table 2. Given these results, we proceeded to pool the Howells and Hanihara data for all further comparisons between Paleoindians and late Holocene populations.

The plot of the first three principal component scores for 14 Q-mode variables across all 219 modern samples and Paleoindians is presented in Figure 2a and b. The first three components account for 52.01% of the variation in the original shape data. Components 1–5 have eigenvalues greater than 1 and account for 68.3% of original shape variation. Although there is some separation of regional groups in the plot, with Africans and Australasians on the left portion of Figure 2a and New World and European samples on the right, the primary impression is one of considerable morphological overlap between major geographic regions. This affirms Relethford's (1994) analysis of craniometric variation in the Howells data, which demonstrated that approximately 10% of modern human craniometric variation is among groups, while the remaining 90% is within groups. Several populations are on the periphery of the main cluster of populations, including Eskimo, Easter Island, San Bushmen, Hottentot, Buriat, and Jomon samples. Several Paleoindians can be seen on the left half of the plot, within the space primarily occupied by Australasians, Polynesians, and Africans on components 1 and 2. Others are located near or within the space occupied by Amerindians and Europeans.

Given the excessive within-group variation in Figure 2, we replotted the first two principal components and generated 90% confidence intervals for the samples by region (Fig. 3). Again, the 90% confidence ellipses overlap considerably, but do show some interpretable geographic variation. As many other researchers have observed (Howells, 1973, 1989; Hanihara, 1993, 1996, 1997; Kamminga and Wright, 1988; Neves et al., 1999; Relethford and Harpending, 1994), African and Australian populations tend to occupy the same multivariate space, while

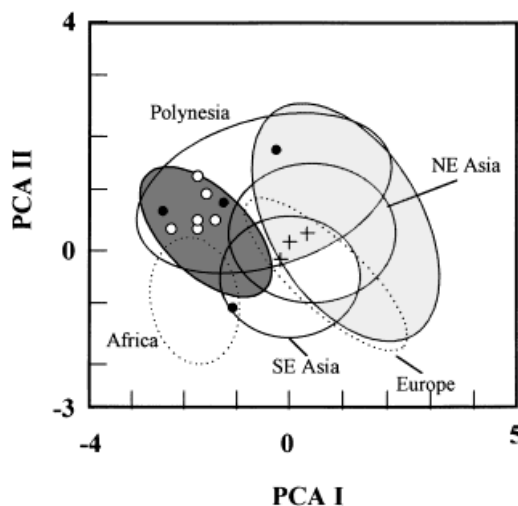


Fig. 3. Ninety percent confidence ellipses for the first two principal components depicted in Figure 1. New World populations in light gray, Australasians in dark gray, all others labeled. Individual North American (solid circles) and South American (open circles) Paleoindians are plotted, as are group centroids for Ainu and Jomon (crosses) samples.

American Indians and Europeans are at the other extreme and Asian populations are intermediate (Fig. 3). Amerindians (gray ellipse) exhibit the greatest range of variation in PCA scores, followed closely by Polynesian populations, and there is nearly complete overlap of the confidence ellipses for American Indians and Europeans.

Table 6 presents the assignments of Paleoindian and Ainu-Jomon groups to modern populations based on 90% and 68% confidence limits for PCA scores. South American Paleoindians all fall within the 90% confidence ellipse for Australian and Polynesian groups. The Santana do Riacho sample is quite close to the Polynesian centroid, indicated by its retention within the Polynesian group when the confidence limit is reduced to just 68%. Lapa Vermelha and one of the individuals from Cerca Grande Abrigo 6 are close to the Australian centroid, as previously observed by Neves et al. (1999b) (Table 6). The North American Paleoindians are much more broadly scattered (Fig. 3), with three samples included in the Polynesian and two included in the Australian 90% ellipses. Only the Wizard's Beach Paleoindian falls within the confidence ellipse for

TABLE 6. *Paleoindian and Ainu-Jomon assignments to modern human populations based on confidence limits of principal component scores*¹

Sample	Africa	Europe	Australia	Polynesia	SE Asia	NE Asia	Americas
North American Paleoindians							
Spirit Cave	0	0	+	++	0	0	0
Wizard's Beach	0	0	0	+	0	0	+
La Brea	0	0	+	+	0	0	0
Warm Mineral Springs	+	0	0	0	+	0	0
South American Paleoindians							
Sta. do Riacho	0	0	+	++	0	0	0
Lapa Vermelha	0	0	++	+	0	0	0
Cerca Grande 6A	0	0	++	+	0	0	0
Cerca Grande 6B	0	0	+	+	0	0	0
Cerca Grande 7A	0	0	+	+	0	0	0
Cerca Grande 7B	0	0	+	0	0	0	0
Ainu-Jomon (centroids)							
Jomon	0	+	0	+	++	+	+
Ainu (Howells)	0	+	0	+	+	++	++
Ainu (Hanihara)	0	+	0	+	++	++	+

¹ 0 = not included in 90% confidence limit; + = included in 90% confidence limit; ++ = included in 68% confidence limit.

TABLE 7. *Bias-corrected Mahalanobis' generalized distances among early and late Holocene populations along the Pacific Rim*¹

	Australasia	Ainu	Paleo	Amerindian	Polynesia	NE Asia	SE Asia	Eskimo
Australasia	0							
Ainu	11.9258	0						
Paleo ²	5.749995	12.76751	0					
Amerindian ³	6.160721	5.488251	6.242881	0				
Polynesia	3.525625	8.943396	3.800986	3.162652	0			
NE Asia	5.676034	5.387965	4.941575	2.277441	2.120086	0		
SE Asia	5.374325	6.057096	6.654686	4.074972	2.643896	1.068646	0	
Eskimo	3.161864	7.958425	1.559785	3.896481	2.109465	1.988475	2.933946	0

¹ Comparative samples for 14 variables in the pooled Howells-Hanihara data.

² Pooled for 11 North and South American specimens.

³ Does not include Northwest Coast samples.

modern New World populations, and Warm Mineral Springs falls within the shared portion of the ellipses for southeast Asia and Africa (Fig. 3 and Table 6). The Ainu-Jomon groups fall within the confidence limits of nearly every reference population except Africa and Australia. The Jomon group is located in the 68% region for southeast Asians, while the Hanihara Ainu fall in the 68% region for both southeast Asians and northeast Asians. The Howells Ainu sample is within the 68% ellipse for northeast Asians and the Americas.

Table 7 presents the bias-corrected Mahalanobis' distances for Pacific rim populations. Paleoindians are clearly closest to Eskimo, followed by Polynesia, northeast Asia, and Australasia. As expected, Amerindians are closest to northeast Asia, followed by Polynesia then Eskimo (Table 7). Typicality probabilities computed from the Mahalanobis' D^2 between each Paleoindian and

reference sample, including two Archaic series, are reported in Table 8. As noted for the PCA plots, the North American Paleoindians have high typicality probabilities for a range of modern human groups, but tend to have highest values for Ainu-Jomon and Polynesian reference groups. South American Paleoindians have consistently high typicality probabilities for Africa and Australasia. The typicality probabilities for Paleoindians relative to the American reference sample were low, with a median value of 0.2265. Only two Paleoindians, Cerca Grande 6B and Wizard's Beach, have a high probability of being included in the American Indian population (Table 8).

Comparison with modern New World samples

In order to examine craniometric variation within the New World, we limited our comparisons to the Amerindian, Pacific

TABLE 8. Typicality probabilities for Paleoindians based on modern regional, Ainu, and Archaic reference samples¹

	La Brea	WMS ²	Wizards	Spirit	Reference sample					
					Sta. Riacho	Lapa Vermelha	CG 6A	CG 6B	CG 7A	CG 7B
Africa	0.0037	0.5388	0.1382	0.4390	0.5653	0.9424	0.7998	0.8622	0.1908	0.0011
Ainu-Jomon	0.0068	0.4892	0.7805	0.7555	0.1836	0.7547	0.6105	0.9586	0.0032	0.0013
America	0.0009	0.3972	0.8045	0.6148	0.0110	0.4202	0.2265	0.7983	0.0230	0.0000
Australasia	0.0016	0.3653	0.5633	0.8854	0.6335	0.9266	0.6973	0.7284	0.2230	0.0002
Europe	0.0208	0.9183	0.2099	0.7318	0.0819	0.7897	0.3255	0.8588	0.0298	0.0006
Indian Knoll	0.0002	0.0304	0.5796	0.3702	0.0653	0.3697	0.1225	0.6605	0.0975	0.0000
NE Asia	0.0100	0.4344	0.4219	0.4288	0.0235	0.5698	0.3936	0.9340	0.0000	0.0000
Polynesia	0.0003	0.3633	0.7601	0.5393	0.0310	0.4995	0.6449	0.9835	0.0286	0.0000
SE Asia	0.0016	0.3153	0.3517	0.3731	0.0256	0.5053	0.3209	0.8440	0.0215	0.0008
Windover	0.0003	0.7768	0.0019	0.2446	0.0000	0.1053	0.0788	0.1909	0.0000	0.0000

¹ Based on ten variables listed in Table 2; **bold** indicates highest typicality probability for a column.

² Key to abbreviations: WMS = Warm Mineral Springs; Wizards = Wizard's Beach; Spirit = Spirit Cave; CG = Cerca Grande.

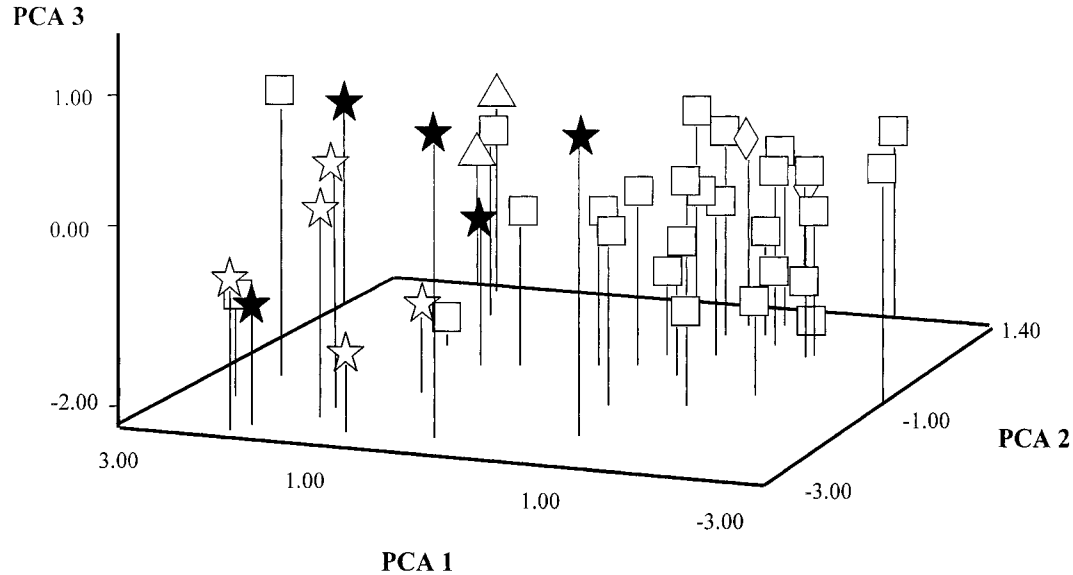


Fig. 4. Principal component plot of early and late Holocene populations in the Americas, using 14 craniometric variables. The first three components account for 53% of the variation in the original size-corrected data. Amerindians (square), Pacific Northwest (diamond), and Eskimo (triangle) centroids are presented, as are individual North (solid star) and South American (open star) Paleoindian specimens.

Northwest, and Eskimo samples listed in Table 3. The ordination of the first three principal components, which account for 53.1% of the original shape variation, is presented in Figure 4. North and South American Paleoindian samples are located in the far left side of the plot, as are Eskimo and some Amerindian groups including a sample from Tierra del Fuego (Fig. 4). The similarity of Paleoindians and Eskimo populations on the first principal component is also reflected in the Mahalanobis' distances

in Table 7. However, the Eskimo groups are separated from most Paleoindians on the second component (Fig. 4). South American Paleoindians are more tightly grouped than North American early Holocene samples, which may reflect reduced variation within the South American Paleoindians. The two late Holocene samples from the Pacific Northwest are within the multivariate space occupied by Amerindians, and were located within the 90% confidence interval for Amerindian PCA scores (not shown).

TABLE 9. Mahalanobis' D^2 values for individual Paleoindian specimens¹

	La Brea	Lapa Vermelha	CG 6A	CG 6B	CG 7A	CG 7B	WMS	Wizard	Sta. Riacho	Spirit
La Brea	0									
Lapa Vermelha	24.9965	0								
CG 6A	28.5953	3.7898	0							
CG 6B	28.1190	3.2441	1.8346	0						
CG 7A	30.1759	4.7105	3.0933	6.8922	0					
CG 7B	31.9528	4.8326	3.7541	5.3163	2.8557	0				
WMS	26.8054	6.4018	7.2639	8.5101	9.4012	10.9521	0			
Wizard	35.7262	14.0533	8.9931	10.3584	11.2680	13.7349	22.1684	0		
Sta. Riacho	37.4779	6.5907	13.2159	15.8173	11.5737	11.7919	21.4072	18.7267	0	
Spirit	27.1060	5.8098	5.8391	9.7502	5.5948	7.7027	6.3585	9.5726	16.0336	0

¹ Values based on individual dimensions, using the pooled within-groups covariance matrix for 14 variables in the world-wide craniometric data. **Bold** indicates significance at $P \leq 0.05$ based on the criterion of Defrise-Gussenhoven (1967). See Table 8 for key to abbreviations.

Comparison of early and middle Holocene samples

To examine patterns of inter-individual variation among early Holocene crania, we computed Mahalanobis' distances using Eq. (2) and the variance-covariance matrix for all seven modern regional samples. These are presented in Table 9. Relative to late Holocene human cranial variation, Paleoindians exhibit considerable phenotypic variation, although the South American samples have smaller distances between individuals than do early Holocene North Americans. The average inter-individual Mahalanobis' distance was 13.34. Under the Defrise-Gussenhoven (1967) criterion, all but eight of the pairwise Paleoindian comparisons (82%) were statistically significant. This appears to suggest considerable heterogeneity among individuals in the Paleoindian sample. However, when the Monte Carlo method was used to simulate a random draw of ten individuals from a recognized modern population (Easter Island), all but one of the replicates had at least 82% significant pairwise differences, with an average of 93% per sample exhibiting significant distances under the Defrise-Gussenhoven (1967) criterion. The average inter-individual distance for the Easter Island series was 19.07, slightly higher than the average Paleoindian distance. These results suggest that despite inter-individual differences in the Paleoindian sample, it is less variable than samples of similar size drawn at random from prehistoric Easter Island (probability observed > simulated $P = 0.9999$). They may also indicate that the Defrise-Gussen-

hoven (1967) criterion is not sufficient to determine the number of populations represented in samples of human crania, given that the Easter Island series is thought to represent an isolated and interbreeding group of humans (Stefan, in press).

Multidimensional scaling of the distances resulted in Figure 5. The South American Paleoindian samples are the most tightly grouped in the plot, while North American Paleoindian and Archaic samples have greater distances among observations. The La Brea Paleoindian specimen is an outlier relative to other early and middle Holocene groups. In general, the specimens in Figure 5 can be roughly divided from left to right by increasing distance from the equator (either north or south). The samples closest to the equator, primarily from the southeastern United States (SE Archaic, Windover, Bird Island, Warm Mineral Springs) are grouped on the left side of the plot. Samples from central latitudes (Plains Archaic, Spirit Cave and Wizard's Beach, Lapa Vermelha, and Cerca Grande) are near the center of the plot. The more northerly Archaic individual from Sauk Valley, Minnesota is located to the right of the plot.

Despite the possible morphological differentiation of Paleoindian data presented in Table 9, we pooled samples represented in Tables 1 and 3 into composite Paleoindian and Archaic cranial series in order to comparison of means and variances of these samples. Only eight variables were used to maximize the data matrix for multivariate analysis of variance (MANOVA) tests (Table

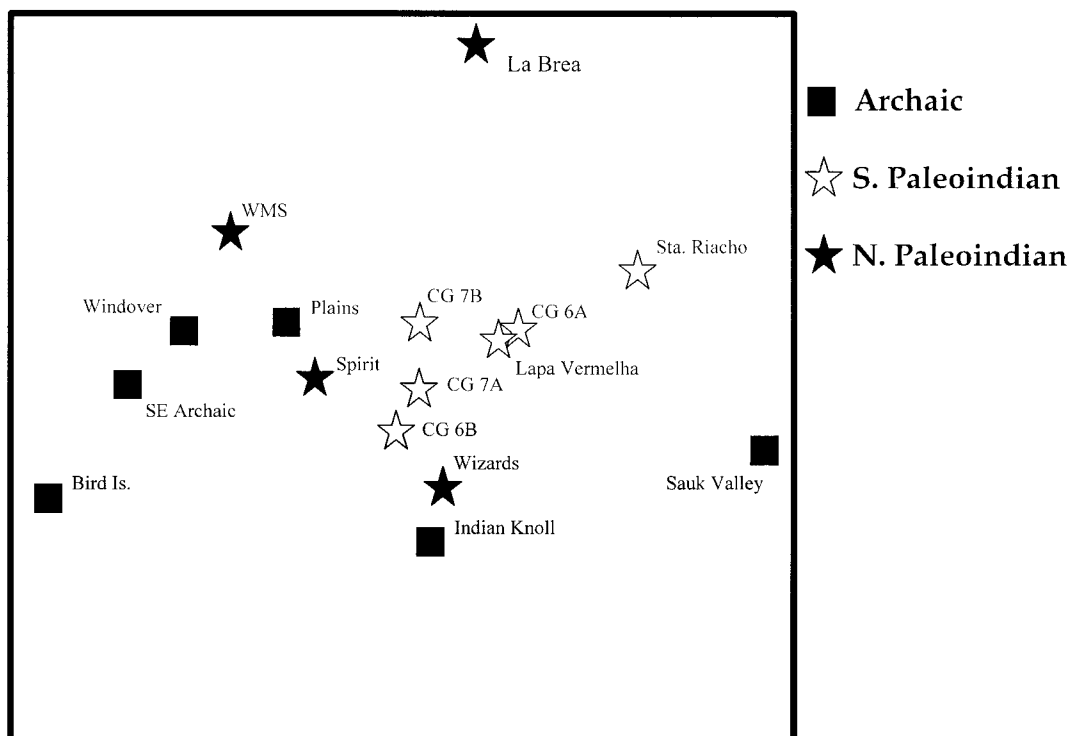


Fig. 5. Multidimensional scaling of Mahalanobis' distances between individual Paleoindian samples and Archaic centroids, using the pooled Howells-Hanihara covariance matrix.

TABLE 10. ANOVA, Levene's test, and MANOVA results for Paleoindian and Archaic samples¹

Comparison	Variable ⁴	ANOVA			Levene		
		<i>F</i>	d.f.	<i>p</i> -value ²	<i>F</i>	d.f.	<i>P</i> -value ²
Paleoindians, Archaics ³	GOL	6.41	1,144	0.0952	4.18	1,144	0.2943
	XCB	1.25	1,144	0.9152	1.03	1,144	0.9493
	ZYB	7.86	1,144	0.0451	1.19	1,144	0.9252
	NLB	2.12	1,144	0.7212	0.39	1,144	0.9977
	OBH	0.6	1,144	0.9903	1.19	1,144	0.9249
	DKB	2.63	1,144	0.5958	0.35	1,144	0.9985
	FRC	1.04	1,144	0.9483	0.01	1,144	1.0000
	PAC	0.53	1,144	0.9936	0.67	1,144	0.9860

¹ Paleoindians pooled for 11 North and South American samples.

² All *P*-values adjusted for familywise error.

³ MANOVA results for all 10 variables: Wilks' Lambda = 0.8545, *F* = 2.9150, d.f. = 8, 137, *P* = 0.0049.

⁴ See Table 2 for key to variable abbreviations.

10). The ANOVA results indicate that only one variable, bizygomatic breadth (ZYB), was different between the two time periods (Table 10). The MANOVA results were significant for these eight variables. Levene's test was not significant for any of the eight variables. When the South American Paleoindian samples are removed, none of the univariate and multivariate comparisons were

significant (Wilks' lambda = 0.9375 *F* = 1.1152, d.f. = 8, 110, *p* = 0.3587).

Typicality probabilities of Paleoindians having been drawn from the Indian Knoll and Windover series, the two most complete Archaic groups for the ten variables examined, revealed that two specimens had a high probability of being "typical" of the Archaic reference groups (Table 8). The

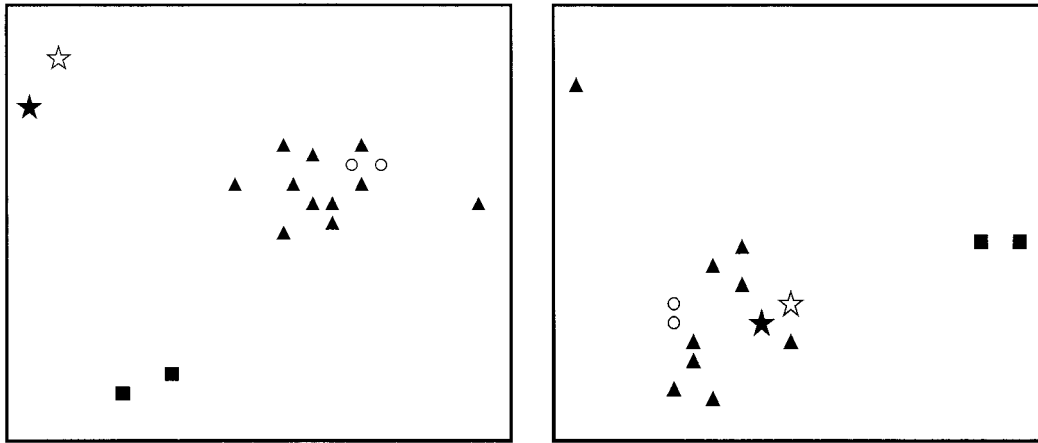


Fig. 6. Principal coordinates ordination of New World samples using R matrix data from the Relethford-Blangero analysis. **Left:** Unscaled plot with all long-term effective population sizes (N_e) set to a relative value of 1. **Right:** Plot of scaled distances (right) using $N_e = 0.30$ for Paleoindians and $N_e = 1$ for all late Holocene samples. North American Paleoindians, solid star; South American Paleoindians, open star; Amerindians, diamond; Pacific Northwest, open circle; Eskimo, solid square.

Warm Mineral Springs female, from northern Florida, has a 78% probability of being drawn from the Archaic sample from Windover, Florida. Other Paleoindians exhibit low to moderate typicality probabilities (0.0002 to 0.57) of having been drawn from either Indian Knoll or Windover. The La Brea female has nearly a zero probability of having been derived from any of the modern reference samples, let alone from New World Archaic groups (Table 8).

MIGRATIONIST INTERPRETATIONS

How do we interpret these results in light of migration/founder models? The Paleoindian samples from North and South America are quite distinct (with a few exceptions) from late Holocene American Indian populations. Paleoindians appear as multivariate outliers in our analyses, and fall closer to the regional centroid of Polynesian and even Australian populations than to modern American or northeast Asian populations. South American Paleoindian specimens form a much tighter grouping in multivariate space than do North American Paleoindians (Fig. 3), and have high typicality probabilities relative to African and Australian comparative samples (Table 8). This phenomenon was noted by a number of early researchers including Keith and Ten Kate,

who suggested a Melanesian role in peopling of the Americas, an idea firmly criticized by Hrdlicka (1935). The results presented here support our previous research, and indicate that South American Paleoindians were more similar to Australasian and even African samples than to modern Amerindians from south of the equator. Neves and coworkers (1996a,b, 1997) and Munford et al. (1995) also noted that lowland Paleoindians are clearly distinct from later Archaic populations in the region. We did observe however, that the Hanihara sample from Tierra del Fuego, Chile was most similar to South American Paleoindian samples (Fig. 4). The North American Paleoindians present a somewhat different picture, with greater internal diversity illustrated in their multivariate dispersion relative to world-wide (Fig. 3) and New World (Figs. 4 and 6) samples. However, our results suggest that the North Americans are more similar to some Archaic samples, as in the case of typicality probabilities for Northwest Coast and Warm Mineral Springs individuals (Table 8). In assessing late Holocene cranio-metric variation in the Americas, we observe that there is considerable within-group diversity. The 90% ellipses for PCA scores show that New World populations overlap Europeans and to a lesser extent northern Asians,

Polynesians, and southern Asians. The Amerindian samples are the most morphologically variable (Fig. 4), which is not surprising given that they represent populations distributed from Canada to Chile.

One way to interpret the morphological divergence of Paleoindians from later Holocene populations in the New World is as a reflection of prehistoric population history. In other words, the data appear to strongly support migration models in which Paleoindians are morphologically (and presumably genetically) distinct from all later Holocene populations in the Americas because they represent a founding population that either did not survive or contributed little to the craniofacial morphology of modern American Indians. This view has been suggested by a number of other morphological studies (Lahr, 1995, 1996; Munford et al., 1995; Neves et al., 1996a,b, 1997, 1998, 1999a,b; Jantz and Owsley, 1998). Lahr (1995, 1996, 1997) and Neves and Pucciarelli (1989) have suggested that the lack of "typical Mongoloid" features in early American crania indicates that they entered the New World prior to the arrival of the "classical Mongoloid" ancestors of living New World natives (Munford et al., 1996; Neves et al., 1997, 1999b).

While a model of multiple migrations from the Old World appears to account for the pattern of observed variation in early crania, it requires making a number of important assumptions. As noted above, this interpretation assumes that morphological variation must have originated in the Old World prior to colonization. It also assumes that the founding populations were distinct in the Old World, and have remained so throughout their tenure in the New World. Thus any differences among New World crania must reflect multiple founding events (i.e., waves of migration) of distinguishable Old World populations. The migrationist interpretation also assumes that *in situ* population structure plays a limited role in creating variation present within and between New World populations. Most importantly, all post-founding populations are assumed to have grown rapidly, so that each late Holocene group has the same long-term effective population size and so that ancient variation is reflected in modern diversity

rather than it being the result of genetic drift. Thus, the association between modern American Indians and northeast Asian "Mongoloids" can be interpreted historically as recent common ancestry, followed by the migration of American Indian founders. The affinity of Paleoindians with southern Asian and Pacific groups reflects their closer shared ancestry, and can be used to suggest that Paleoindians represent a separate founding population distinct from that which gave rise to living American Indians, provided all of the above assumptions hold.

THE PEOPLING OF THE NEW WORLD: EFFECTS OF PREHISTORIC POPULATION STRUCTURE

Model-bound methods

In our previous research (Neves et al., 1996a,b, 1997, 1998, 1999a,b; Powell and Steele, 1993; Steele and Powell, 1994) we have interpreted these results using the assumptions of migrationist models. To test the assumptions of migration models, we examined the Paleoindian and New World data using model-bound approaches, which provide estimates of population parameters not possible in model-free methods (Relethford and Lees, 1982). Model-bound analyses make explicit assumptions regarding the mode of transmission of underlying genotypic variation, the amount of genotypic variation expressed in the phenotype, and evolutionary and demographic parameters affecting population structure. This approach has been applied to craniometric variation among present (Konigsberg and Blangero, 1993; Relethford, 1994, 1995; Relethford and Harpending, 1994, 1995) and past (Donnelly and Konigsberg, 1998) hominids, and has been particularly helpful in clarifying problems of interpretation in model-free analyses.

There are a number of serious difficulties in applying the model-bound approach to samples from different time periods. Models assume that the effective population size of all groups is known or can be estimated, and that the samples are contemporaneous and therefore had the potential to exchange genes through short-range gene flow. For Paleoindians, we know little about the demographic structure or effective population size of these

groups. Further, Paleoindians are separated from modern samples by at least 350 generations, and from each other by as much as 80 generations, which makes it difficult to infer patterns of past gene flow. However, model-bound analyses have been applied to diachronic samples of prehistoric remains (Konigsberg, 1988, 1990; Powell, 1995; Steadman, 1998), though most of these series represent no more than 40 generations between samples.

Given these problems, we use the model-bound approach simply as a *heuristic device*, with attention to how the samples may or may not meet stated assumptions, and how alteration of model parameters affect the pattern of genetic relationships observed. From these data we can estimate variance parameters for modern reference samples that *do* meet the requisite assumption, then observe the effects of adding Paleoindians to the analysis. One justification for using model-bound approaches with the Paleoindian data is that many models of New World colonization assume that modern population structure is a reflection of substructure among prehistoric groups, through "freezing" of population structure by rapid demographic growth (Mosimann and Martin, 1975) followed by minimal gene flow between regions. Several authors (Lahr, 1995, 1996, 1997; Munford et al., 1995; Turner, 1985) have asserted that there has been insufficient time since initial colonization for evolutionary processes to act on American Indian phenotypes. These assumptions provide a starting point for examining how patterns of phenotypic variance among past and present populations in the New World might be affected by altering the assumptions of the models.

Relethford and Blangero (1990) developed a method of analyzing variation within and among populations using phenotypic traits under the assumption of panmixia, based on the **R** matrix approach of Harpending and Ward (1982). To conduct this analysis, the Q-mode data were converted to a g by t matrix of deviations of group means from weighted total means, Δ . An estimate of average heritability for craniofacial traits of $h^2 = 0.55$ obtained by Devor (1987) has been used in several other studies (Donnelly and Konigsberg, 1998; Relethford, 1994, 1995; Relethford and Harpending, 1994) to produce

an estimate of the additive genetic variance-covariance matrix (**G**) based on values in the phenotypic variance-covariance matrix (**P**). Relethford and Blangero (1990) found that the analysis is relatively robust under a wide range of average heritability estimates. Using the relationship $\mathbf{G} = h^2\mathbf{P}$, we then computed the codivergence matrix, **C** as

$$\mathbf{C} = \Delta \mathbf{G}^{-1} \Delta' \quad (3)$$

where \mathbf{G}^{-1} is the inverse of the t by t pooled within-group additive genetic variance-covariance matrix averaged over all populations and weighted by population size (Blangero, 1990; Relethford and Blangero, 1990; Relethford and Harpending, 1994). The codivergence matrix divided by t provides an average over all traits (\mathbf{C}/t). Wright's (1951) familiar measure of among-group genetic variance, F_{ST} , can be represented as the average genetic distance to the centroid

$$F_{ST} = \frac{\sum_{i=1}^g w_i \mathbf{C}_{ii}}{\left(2t + \sum_{i=1}^g w_i \mathbf{C}_{ii}\right)} \quad (4)$$

where g is the number of subdivisions, t is the number of traits, w_i is the sample weight of the i th sample. Low values of F_{ST} indicate limited among-group variation genetic variation relative to total variation under panmixia. The **R** matrix is given as

$$\mathbf{R} = \frac{\mathbf{C}(1 - F_{ST})}{2t}. \quad (5)$$

Initially, sample weights of $1/g$ were used for computations, but analyses were repeated using different weighting factors to determine the effects of different long-term effective sizes on the results.

The diagonal elements of the **R** matrix, r_{ii} , represent the genetic distance of population i to a regional centroid, so that genetic distances between populations are obtained as $d_{ij} = r_{ii} + r_{jj} - 2r_{ij}$ (Harpending and Jenkins, 1973). All distances were corrected for sample bias, and estimates of standard errors for F_{ST} and other statistics were generated following Relethford and co-workers (1997). Estimates of long-term effective population size were used to produce a scaled **R**

TABLE 11. F_{ST} values for early and late Holocene New World samples

Grouping	Populations	Observations	F_{ST}	SE
Late Holocene populations				
Amerindians	11	445	0.1274	0.0129
Eskimo ¹	2	110	0.0873	0.0113
Amerindians and Eskimo	13	645	0.1606	0.0107
Pacific Northwest ¹	2	49	0.1037	0.0122
Amerindians and Pacific Northwest	13	494	0.1188	0.0113
Pacific Northwest and Eskimo	4	294	0.1801	0.0111
Native Americans (total)	15	694	0.1530	0.0095
Early-Late Holocene populations				
Amerindians and Paleoindians	13	457	0.1650	0.0136
Eskimo and Paleoindians	4	212	0.1556	0.0213
Pacific Northwest and Paleoindians	4	61	0.3407	0.0185
Native Americans and Paleoindians	17	706	0.1739	0.0107

¹ F_{ST} derived from pairwise Mahalanobis distance following Konigsberg and Blangero (1993).

matrix following Relethford and Harpending (1995). The scaled \mathbf{R} matrix eliminates the potential effects of genetic drift on genetic distances, although it assumes that the populations are at equilibrium population structure, an assumption that may not hold for these data. However, genetic distances converge more rapidly than other population parameters (Relethford, 1996; Wood, 1986), so the relative distances among samples may be accurate even when the true magnitudes of the distances may be underestimated.

The Relethford-Blangero (1990) model is used here to detect deviations from an equilibrium between gene flow and genetic drift derived from observed (\bar{v}_i) and expected [$E(\bar{v})$] values of within-group phenotypic variance. Residual within-group variances were calculated as

$$R(\bar{v}_i) = \bar{v}_i - E(\bar{v}_i). \quad (6)$$

The model assumes that effective population sizes are known or can be estimated. The standard errors of residual variance were obtained using jackknifing across t variables (Miller, 1974). The residual divided by its standard error is distributed as a t -statistic with $t - 1$ degrees of freedom (d.f.) = $t - 1 = 13$, which provides a test of significance for the residual variances. Under the Relethford-Blangero model, positive residuals for a particular population may reflect: (a) higher levels of long-range gene flow from an "outside" source (Relethford and Blangero, 1990), resulting in greater heterozygosity; (b) a higher mutation rate than other groups considered; (c) a larger effective population

size or different timing of population growth than other populations (Relethford, 1995); (d) nonrandom sampling effects or population pooling that artificially inflate within-group variance.

Model-bound results

F_{ST} values provide a method of examining between-group variation in the New World samples. Under the assumption that all long-term effective sizes were the same, we obtained the values of F_{ST} presented in Table 11. The two Eskimo samples exhibit the lowest F_{ST} value, followed by the Pacific Northwest and Amerindian samples. Interestingly, the Amerindian-Pacific Northwest pair has a lower F_{ST} (0.1188) than either the Amerindian-Eskimo (0.1606) or Eskimo-Pacific (0.1801) groupings. This supports the PCA analyses of between-group variation presented in Figure 4. The total New World F_{ST} is 0.1530, which is within the range of F_{ST} values (0.04 to 0.16) obtained for New World *Alu* insertion data (Novick et al., 1998).

One potential problem is that the number of variables and the number of subdivisions within regions has an impact on values of F_{ST} . For example, Relethford (1994) used 57 variables for 18 populations in the Howells data grouped into three (major "races") and six (major geographic regions) subdivisions, and found that for three groups $F_{ST} = 0.065$, which increased to $F_{ST} = 0.085$ for six subdivisions. When we repeated Relethford's (1994) six subdivision analysis on Howells' data using only the 14 variables employed in the present study, we obtained an F_{ST} value

TABLE 12. Genetic distances to the centroid and observed, expected, and residual variances for early and late Holocene New World populations

Population	r(ii)	Observed variance	Expected variance	Residual	SE	<i>t</i> (d.f. = 13)	<i>P</i> (adj)
Arikara	0.1444	0.724	0.923	-0.199	0.017	11.779	0.0000
StaCruz	0.1270	0.608	0.942	-0.334	0.013	26.353	0.0000
Peru	0.1136	0.754	0.956	-0.202	0.021	9.769	0.0000
California	0.0811	1.076	0.991	0.085	0.034	2.515	0.3593
Columbia	0.1631	0.898	0.903	-0.005	0.043	0.116	1.0000
Fuegan	0.0708	0.823	1.002	-0.179	0.030	6.012	0.0007
Iroquois	0.1350	0.811	0.933	-0.122	0.026	4.661	0.0075
Northeast	0.1647	0.647	0.901	-0.254	0.019	13.484	0.0000
Oregon	0.2276	0.678	0.833	-0.155	0.031	4.925	0.0047
Peru2	0.1155	0.773	0.954	-0.181	0.017	10.480	0.0000
Venez	0.5317	0.746	0.505	0.240	0.043	5.530	0.0016
BritCol	0.1471	0.765	0.920	-0.155	0.027	5.657	0.0013
NWCcoast	0.1334	1.045	0.935	0.110	0.041	2.658	0.2870
Eskimo (Howells)	0.3917	0.773	0.656	0.116	0.010	11.150	0.0000
Eskimo (Hanihara)	0.2663	0.781	0.791	-0.011	0.022	0.495	1.0000
NA Paleoindian	0.2913	1.753	0.764	0.989	0.114	8.697	0.0000
SA Paleoindian	0.5719	0.718	0.462	0.257	0.062	4.130	0.0200

of 0.196; for 18 subdivisions and 14 variables, F_{ST} was 0.251. Merriwether et al. (1995) observed that the Eskimo/Pacific Northwest F_{ST} s derived from mtDNA were in the range of 0.01 to 0.07 (adjusted for the haploid inheritance of mtDNA). They also note that North American samples produced lower values of F_{ST} when paired with Pacific Northwest than did South Americans, and that pairwise F_{ST} values within Amerindians were in the range of 0.00 to 0.0925, somewhat lower than the values obtained for craniometric variation. The craniometric data presented here are consistent in a relative way with the mtDNA observations of Merriwether et al. (1995), although the absolute values of F_{ST} for craniometrics were higher in all cases after adjusting for haploid inheritance of mtDNA.

Given that the pattern of among-group variation in late Holocene New World samples is generally consistent with patterns observed for genetic data, we produced F_{ST} values between Paleoindians and late Holocene samples as a means of assessing how among-group variances changed when ancient samples were added. As expected for groups separated in time, the addition of early Holocene samples inflated the F_{ST} values slightly (Table 11). However, all F_{ST} s except for the Pacific Northwest-Paleoindian comparisons are below the value of 0.20 used as an indication of interbreeding subpopulations under an island model of migra-

tion (Wright, 1951). These values are also within the range reported by Jorde (1980) for major intracontinental subdivisions of modern humans. While we realize that modern and late Holocene populations had no chance to interbreed in actuality, the values of F_{ST} provide an estimate of how extreme among-group divergence may have been. Donnelly and Konigsberg (1998) applied this method to Neandertals and modern human samples, noting that the values of F_{ST} obtained (0.13) were within the range of F_{ST} s seen in modern humans. For our data, it appears that Paleoindians are not divergent relative to modern Amerindian or Eskimo populations, but have a larger F_{ST} when compared to the small Pacific Northwest sample.

We performed the Relethford-Blangero analysis, restricting our focus to 13 late Holocene New World populations. The initial analysis assumed equal relative effective sizes for all samples, and an average craniometric heritability of 0.55 (Devor, 1987). The F_{ST} obtained was 0.1530 ± 0.009 , and the average within-group variance was 0.806. None of the late Holocene samples deviated significantly from the expected model at the $p = 0.05$ level of comparison. Thus, it would appear that the assumptions regarding effective population sizes are acceptable in this case.

Table 12 presents the results of a Relethford-Blangero analysis on the same

late Holocene data, with North and South American Paleoindians added. The same assumption regarding equal effective population size was employed. In this case, the addition of the early Holocene samples altered the pattern observed in the previous analysis, so that all but four samples (California, Columbia, Northwest Coast, and Eskimo) exhibit statistically significant deviations from expected within-group variation (Table 12). Average within-group variation has increased from 0.804 to 0.845, and most samples have negative residual values except for North and South American Paleoindians, California, Northwest Coast, and Eskimo. The plot of the **R** matrix is provided in Figure 6a, and shows that both Eskimo and Paleoindian samples are clearly separated from other New World populations. This is exactly the result obtained from the PCA analyses of craniometric shape (Fig. 3), and would seem to support the view that Paleoindians represent a biological population distinct from modern American Indians.

To interpret Figure 6a as a reflection of past population history requires assuming that microevolutionary processes, such as genetic drift, did not affect the results. Explicitly, this would entail that all samples have equal effective population sizes, thus eliminating the possibility that the divergence of Paleoindians is a product of genetic drift. While this appears to be valid for the late Holocene samples, how realistic is this assumption for Paleoindians? Steele et al. (1998) provide evidence to suggest that environmental constraints played a role in population growth during the initial settlement of the Americas. Their simulations, based on a wide range of carrying capacities and excessively high rates of movement (250 km per lifetime) produced estimates of initial population size over the period of 13,000–11,000 years B.P. ranging from 1,941 to 554,301 persons in North America. Even using the upper end of their range produces an estimate of 0.023 persons/km², which is well within the range of hunter-gatherer population densities for temperate forest and grassland environments, but lower than estimates for tropical rain forests (Steele et al., 1998). These population density estimates imply *small* average effective popula-

tion sizes (N_e) for Paleoindians. Making the assumption that 5,000 such groups were scattered across North America during the early Holocene results in an estimate of 36 to 100 persons per subpopulation.

We repeated our **R** matrix analysis using relative weights of 1.0 for all modern groups, but an N_e of 0.30 for Paleoindians. This estimate of relative size was derived using the upper end of early Holocene census population size of North American Paleoindians from Steele and co-workers (1998) relative to estimates of late Holocene census size in North America (Ubelaker, 1992). The resulting analysis produced an improvement in the fit of the model, and resulted in $F_{ST} = 0.1549 \pm 0.009$ for all New World populations. A comparison of the ordination of unscaled and scaled **R** matrices (Figure 6a and b) is quite striking. In the scaled plot (Fig. 6b), which accounts for the effects of genetic drift on distances, Paleoindians move much closer to other Amerindian samples and away from Eskimo populations. The Eskimo samples remain divergent from other New World samples (Fig. 6b), which makes it difficult to include these populations in a single-migration model, as has been proposed using mtDNA variation (Merriwether et al., 1995). However, their outlying position may also reflect a smaller long-term effective size among these groups.

These results suggest that the model-free analyses, in which Paleoindians appear to be “outliers” relative to late Holocene New World populations, may be attributed to genetic drift. When higher weights for Paleoindian sample sizes were used, these groups move farther from the main cluster of points in Figure 6b. Under the assumption of smaller long-term effective size, Paleoindian samples are not as divergent as they would be under assumptions of equal effective sizes inherent in model-free analyses.

CONCLUSIONS

How we interpret variation in the Americas depends, in part, on our views on the origin of modern human diversity (Lahr, 1995, 1996; Lahr and Foley, 1998; Relethford and Harpending, 1994, 1995), the rate of macro- and microevolutionary change possible for phenotypic features (Carlson and

Van Gerven, 1977; Eckhardt, 1999), and the meaning of late Pleistocene diversity in the Old World (Brace and Tracer, 1992; Howells, 1989; Kamminga, 1992; Kamminga and Wright, 1988; Lahr, 1996). Most importantly, the assumptions inherent in different models of Pleistocene human expansion and migration can be quite different (Lahr and Foley, 1998), and as we have shown here, can considerably alter our interpretations of past cranial diversity.

Multiple founding events

North American within-group variation may be the result of sampling more than one founding population, thereby artificially inflating within-group variance when distinct populations are pooled as they are here and elsewhere (Steele and Powell, 1992, 1993, 1994). Jantz and Owsley (1998), based on their analysis of early Holocene crania, suggested that at least three populations were represented by the pattern and degree of observed differentiation. Such an observation is also consistent with models that invoke multiple waves of migration, especially those that envision that North and South American populations, or different mtDNA haplogroups, were the products of different waves of migration from Asia (Horai et al., 1993; Munford et al., 1995; Neves et al., 1996a,b, 1997, 1998, 1999a,b; Schanfield, 1992; Schurr et al., 1999; Starikovskaya et al., 1998; Wallace and Torroni, 1992).

Assuming that populations changed little during the past 13,000 years, the results of the model-free analysis appear to support the view that more than one founding population colonized the Americas. However, to make such an interpretation requires assuming equal long-term effective size for all populations, limited diversity within the founding population with subsequent "freezing" of ancient among-group variability through rapid demographic growth, and the morphological distinctiveness of populations in the source area(s) of the Old World. Lahr (1996) and Turner (1985) have observed that the latter assumption appears to be supported in the fossil record of east Asia, and the tripartite model makes explicit reference to strong demographic growth. Such a model of rapid demographic change has

been suggested by the simulation work of Mosimann and Martin (1975).

Population structuring

Alternatively, the North American Paleoindian data may reflect draws from a biological population that was regionally structured, as suggested by O'Rourke et al. (1999), Powell (1995), and Anderson (1996). This differs from the previous explanation because the subdivisions do not necessarily have to constitute separate founding populations, but instead may be subdivisions of a single founding group. If genetic drift had occurred in a small polymorphic founding population (or populations) isolated by geographic barriers (Szathmáry, 1993; Rodgers et al., 1992) or simply by distance (Powell, 1995, 1997), then extreme morphological diversity of Paleoindians relative to late Holocene American Indians may have resulted. North American Paleoindians have a larger geographic dispersion, averaging 2994 km between sites, which may be related to their greater within-group diversity relative to South Americans (Tables 9 and 10 and Figures 4 and 5). South American samples are separated only by an average of 338 km, and exhibit much less within-group diversity (Tables 9 and 12 and Figure 5). The relationship between geographic distribution of samples and measures of biological diversity reported here parallel findings from population genetics, where the most geographically dispersed populations exhibit the greatest between-group variation (Merriwether et al., 1995; Novick et al., 1998). If population structuring processes were acting on founder populations, then a strict interpretation of early diversity as a reflection of population history becomes more difficult to accept, as noted by many other researchers (Felsenstein, 1982; Relethford, 1995, 1999; Relethford and Harpending, 1994, 1995).

Powell (1995, 1997) performed a simulation of genetic variance generated by the peopling of the Americas using the simplifying assumption of island migration and an initial effective population size of $N_e = 50$ for all groups. He observed that, for quantitative traits with 10 loci (assuming a founder population with relatively limited genetic

variation), effective populations sizes and population growth rate during the terminal Pleistocene must have been large (on the order of $r = 0.04$) in order for genetic drift to have played no role in structuring phenotypic variation in the Americas. This level of growth is higher than that seen during the Industrial Revolution, and is comparable to growth occurring among developing nations today (Powell, 1997).

In reality, both population structure, including gene flow and genetic drift, and non-recurrent historical events such as colonization/range expansion are likely causes of the temporal and spatial patterns of craniometric variation in the Americas. In fact, population history and structure are non-mutually exclusive (Templeton 1998a,b; Templeton et al., 1995), although we separated them in this paper to emphasize how the assumptions of each affected the interpretation of our results. Templeton notes that "genetic differentiation between any two human populations may represent a mixture of both gene flow and historical events" (Templeton, 1998b, p 636); gene flow among groups in Asia, and/or Beringia, and/or the New World before, during, and after colonization "events" is not only a complicating factor in recovering population history (Karafet et al., 1999), but is likely to have happened as a part of the colonization process (Powell, 1995). Finally, some of the variation in craniofacial form through time and space may reflect nonphylogenetic information (Steele and Powell, 1992) resulting from developmental constraints (Enlow, 1990), functional morphology of the face, teeth, and jaws (Boyd, 1988; Kean and Houghton, 1990; Carlson and Van Gerven, 1977), and gene-environment interactions (Crawford, 1999; Larsen, 1997).

Our previous research has proceeded using the assumptions of the migrationist models (Neves and Pucciarelli, 1989, 1991; Neves et al., 1996, 1998, 1999a,b; Powell and Steele, 1993). While many other researchers have also made these assumptions (Jantz and Owsley, 1997, in press; Powell and Steele, 1993; Steele and Powell, 1992, 1993, 1994, 1999), we feel that the assumptions are worth putting to the test. Certainly, aspects of the demographic history of New World

populations can be recovered from both modern DNA analyses, from new archaeological discoveries and re-assessment of the existing record, and from analyses of phenotypic variation in American populations through time and space. Anthropologists now have the tools at hand to reconcile these diverse data sets, and must begin by questioning their assumptions in an explicit manner. As Weiss (1994) has noted, better data can improve our resolving power, but to maximize our ability to truly understanding what we are seeing will require not only a synthesis of existing data, but integration of a wide variety of new information from all fields of anthropological investigation. We hope that by bringing an evolutionary and process-oriented approach to bear on the early skeletal record in the Americas, we can improve our understanding of the pattern and process of the peopling of the New World.

ACKNOWLEDGMENTS

We thank Chris Ruff for the invitation to write this article, and Gentry Steele, Richard Jantz, Betsy Schumann, Erik Trinkaus, Ann Carson, Erik Ozolins, Megan Rhoads, Steve Zegura, Bruce Huckell, and the anonymous reviewers, Frank McManamon, and Russell Nelson for thought-provoking discussions and suggestions about the concepts presented in this paper. While we benefited from the input of our colleagues, they are blameless for any errors or omissions presented here. We are especially indebted to Tsunihiko Hanihara for allowing us to use his extensive comparative data, and to W.W. Howells for making his data available via the Internet. We also thank the staff and curators of the following institutions for allowing us to examine Paleoindian and Archaic skeletons in their care: Florida State University; Illinois State Museum; Museu Nacional, Rio de Janeiro; Nevada State Museum; Southern Illinois University, Carbondale; Strecker Museum; Texas A&M University; Universidade de Sao Paulo; Universidade Federal de Minas Gerais; University of Florida; University of Tennessee. We are deeply appreciative of the assistance of Ann Carson and Leah Carson Powell in preparing the final version of the manuscript. The research presented here was supported by

funds from the L.S.B. Leakey Foundation (Grant No. 5666), the Wenner-Gren Foundation for Anthropological Research, and the University of New Mexico (Grants RAC 194–1997 and RAC 216–1999) to JFP, and a FAPESP grant (Grant No. 97/3210–1) to JFP and WAN. During the writing of this paper WAN was supported by a CNPq scholarship, and JFP was supported by the Katherine Woodson Endowment and a UNM Research Semester award.

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